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The Muscular System of the Red Howling Monkey

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The Johns Hopkins University
School of Medicine

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Director, United States National Museum

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The Muscular System of the Red Howling Monkey

Introduction

The howling monkeys, which are members of the superfamily Ceboidea (Simpson, 1945), inhabit a very extensive area in the tropical and subtropical forests of Central and South America. They are well known among travelers and naturalists for their prodigious roars, which can be heard for very long distances. The voice-producing organs have been extensively studied in the past. The pertinent bibliography can be found in the summary account of Starck and Schneider (1960) and the recent study by Kelemen and Sade (1960). Schön (1964a) added further information about the pharyngolingual musculature of this animal and emphasized certain functional aspects of these structures. The muscular system of the whole animal was investigated by Santi Sirena (1871), who compared it with man, the great apes, and some catarrhine monkeys; unfortunately, this work has remained little known among modern students of primate anatomy. Sirena used three specimens preserved in alcohol. They were tentatively classified as *Mycetes fuscus*, a synonym for the accepted name *Alouatta fusca* (Hershkovitz, 1964). Two were males, but Sirena could not ascertain the sex of the other animal because its genito-urinary organs had been removed. Each one had fourteen pairs of ribs, and at least one was an adult.

The purpose of my research was to compare the entire muscular system of *Alouatta* with that of the spider, woolly, and woolly spider monkeys, on the one hand, and the capuchin on the other. All of these animals have prehensile tails. The howler is usually grouped with *Ateles*, *Lagothrix*, and *Brachyteles* as a brachiator (Erikson, 1963) or as a semibrachiator (Ashton and Oxnard, 1963). *Cebus* is classified as a climber (Erikson, 1963) or as a quadruped (Ashton and Oxnard, 1963). It is hoped that by contrasting the differences and similarities between the howling monkey and the other four, the muscular adap-

tations of *Alouatta* which have permitted this genus to follow its own evolutionary path will become evident.

Four enbalmed specimens of the red howling monkey (*Alouatta seniculus*) were dissected under an Aloe Dazor fluorescent lamp with a magnifier head. Three were adult males, two from central (Guárico State) Venezuela, and one from eastern (Delta Amacuro Territory) Venezuela. The adult female was obtained through animal dealers centered in Leticia, Colombia. In addition, the masticatory and palatine muscles on the severed heads of two young adult females and one adult male from central Venezuela were studied. The ventral neck muscles were also observed in this male. It was not possible to observe the facial and dorsal trunk muscles in the female because they had been damaged while removing the brain and spinal cord. In the following account all this information has been pulled together. Variations are indicated wherever present.

The data are organized according to a slightly modified version of a scheme developed by W. L. Straus, Jr. (unpublished), which is based on his own experience and on the previous work of A. B. Howell (1936, 1939). The recently approved Nomina Anatomica (1966) has been employed, but other commonly known anatomical terms have occasionally been used. To facilitate the comparison of the facial musculature of the howler with that of the Atelinae and *Cebus*, I have adhered to the terminology used by Schreiber (1928) and Huber (1930, 1931, 1933). It was found that some former students called their specimens by names accepted today only as synonyms. These are followed in this text by a parenthesis containing the name which is now accepted. In this work every muscle is first described and comments are added about observations made by other authors on the same structure of *Alouatta*. This is followed by the innervation and inferences about the function. The latter were based on the topographical arrangement and on what is presumed to be the action of the particular muscle in man or other primates (Howell and Straus, 1933). Finally, the comparative anatomy is reviewed. Sometimes groups of muscles are treated together in relation to functional and comparative aspects.

This work is based on the dissertation presented by the author to the Graduate Board of the Johns Hopkins University in partial fulfillment of the requirements for the degree of Doctor of Philosophy, June 1966. It was aided in part by a training grant from the National Institutes of Health.

I wish to express my appreciation to Dr. W. L. Straus, Jr., Department of Anatomy, Johns Hopkins University School of Medicine, for his guidance and indispensable advice, and to Dr. D. Bodian, Chairman of that Department, who arranged for financial support.

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Muscles of the Head

Trigeminal Group

M. temporalis: It is an extensive but not very thick triangular muscle whose base corresponds to the linea temporalis and lambdoid crest, the apex to the insertion on the mandible (fig. 1). The linea is more marked in older individuals of both sexes where it is seen as a long, sharp ridge extending from about the middle of the lambdoid crest to the superciliary arch. Origin of the muscle is by fleshy fibers from (1) the back of the orbit on the facies temporalis of the alisphenoid and frontalis. A crest which follows the sphenomalar articulation is occasionally seen at the point of attachment of these fibers; (2) the entire medial wall of the temporal fossa where its fibers ascend to the temporal line; (3) the lambdoid crest; and (4) the cranial side of the transverse root of the zygoma. Finally, (5) many bundles come from the caudal half of the inner surface of the temporal aponeurosis and also invade the jugal arch on its deep aspect. Anterior fibers are almost vertical while those of more dorsal location are increasingly oblique until they become almost horizontal and forwardly directed when the origin is from the lower part of the lambdoid crest and transverse root of the zygoma. A central tendon is formed within the sagittal plane of the muscle and divides it into a superficially thicker and a deep thinner part. Starck (1933) says that the tendon is covered by two-thirds of the fleshy mass. Insertion of the muscular fibers takes place on both aspects of the coronoid process (fig. 2) and the tendon. This last ends on the margins of the bony eminence. Some of the tendinous fascicles continue distally as a lateral and a medial bundle attached to the margins of the retromolar fossa. Starck (1933) found in three specimens of *A.* (*Mycetes*) *auratus* (=*Alouatta seniculus*) that the temporalis was almost twice as large in the adult male (21.0 g.) as in the adult female (13.5 g.) and ten times that of the juvenile (2.1 g.). Sirena (1871) remarks on the large size of the muscle in *Alouatta fusca.*

Nerve supply: The anterior division of the mandibular nerve.

Function: Elevator and retractor of the mandible.

M. masseter (fig. 1): This strong muscle is incompletely divided from behind forward by a sagittal cleft into a superficial and a deep portion. They are united into a single mass only in the anterior half of the belly.

Pars superficialis is the larger of the two parts. Its origin is on the external surface and lower margin of the entire zygomatic arch. Anterior fibers are initially tendinous and firmly anchored to the bone.

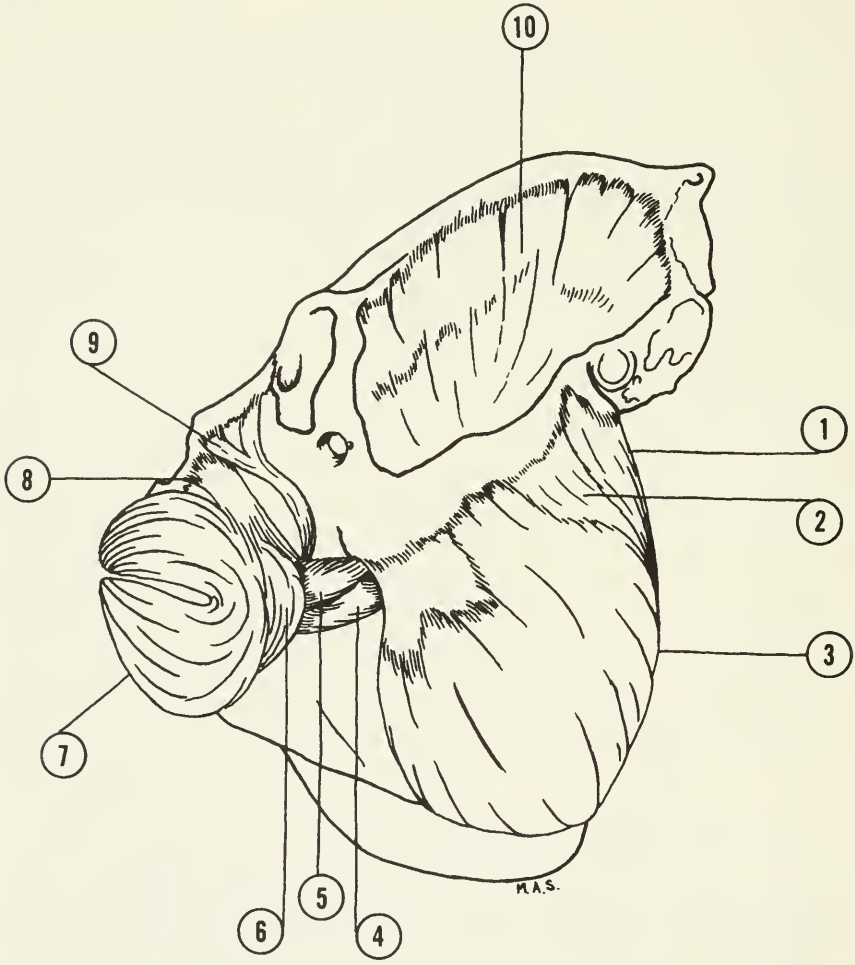

FIGURE 1.—Masticatory and facial muscles (1, capsule of temporomandibular joint; 2, aponeurotic part of the pars superficialis in continuity with the capsule of the joint; 3, m. masseter; 4, deep layer of m. buccinator; 5, its intermediate layer; 6, its superficial vertical layer; 7, m. orbicularis oris; 8, m. caninus; 9, m. maxillo-naso-labialis; 10, m. temporalis).

A tubercle, a depression, a roughened area or a sharp short crest can be seen at this point in the zygomatic process of the maxilla. These fascicles form a gleaming lamina in the upper rostral quadrant of the muscle. Their direction is almost vertical along the anterior border, but increasingly oblique as they aim toward the angle and dorsal edge of the ramus. Posterior fibers arise from the rear fourth of the arch. They are muscular at the middle of the zygoma, and aponeurotic nearer to the fossa mandibularis, where they are organized into a thin but resistant sheet which is continuous without interruption with the capsule of the temporomandibular joint. The fleshy fibers reach the basis mandibulae and the margins of the angle and ramus following a progressively more horizontal direction. They are connected through a tough fibrous raphe with those of m. pterygoideus medialis. Deeper bundles fasten to most of the lower three-fourths of the external surface of the ramus. The orally concave rostral margin of the muscle covers the second upper molar, a fact already indicated by Starck (1933). The mandible of strong males has a depression corresponding to the insertion of the deeper fibers.

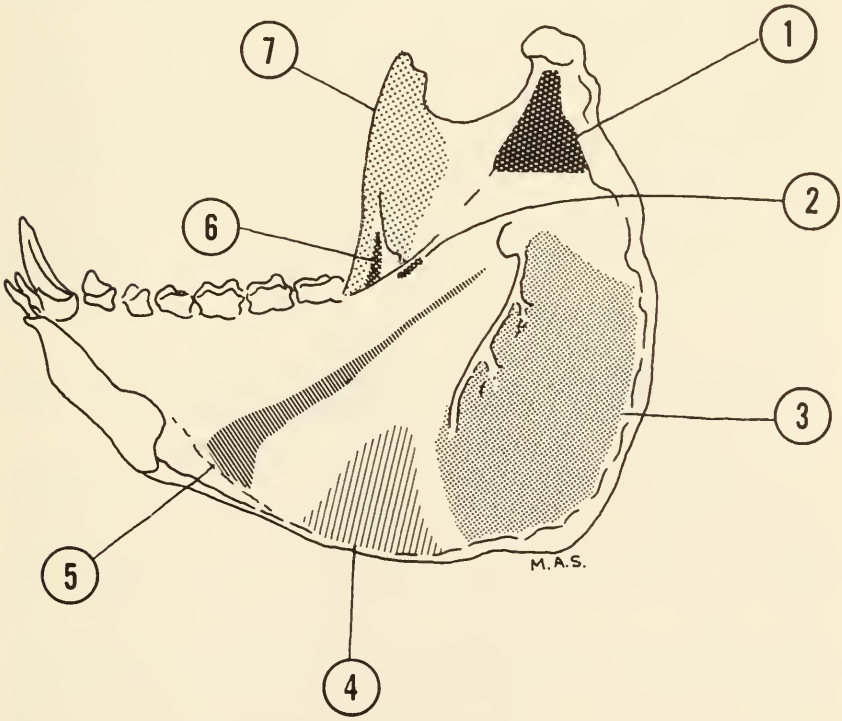

FIGURE 2.—Muscular attachments in the mandible (1, m. pterygoideus lateralis; 2, m. constrictor pharyngis superior; 3, m. pterygoideus medialis; 4, m. digastricus; 5, m. mylohyoideus; 6, m. buccinator; 7, m. temporalis).

Pars profunda has a fleshy origin from the lower lip and internal surface of the zygomatic arch where, rostrally, the fibers are difficult to separate from those of m. temporalis. A zygomaticomandibular portion (see Starck, 1933) is not identifiable as a separate bundle. This origin occupies in the jugal arch an extension equal to that of the pars superficialis. Profunda fibers are entirely muscular in the anterior three-fourths where they are almost vertical and attach rapidly to the bone. Those of the posterior fourth are superficially tendinous near the ramus but muscular elsewhere. They run down and forward ending after a short course. Insertion of pars profunda is on the upper fourth of the ramus and causes an excavation of the bone below the incisura mandibulae. Between the attachment of the two parts there is a wide area not occupied by muscular insertion. A few tendinous strands developed within the substance of the masseter, especially where pars superficialis and profunda form a single mass, fasten to the ramus together with the fleshy bundles.

According to Leche (1912) the muscle is relatively thicker in the embryo than in the adult howler and the space between its two parts narrower. He concludes, therefore, that the enlargement of the mandible, which takes place later, must be associated with other factors besides growth of the masseter. Starck (1933) compared the weights of this muscle and the temporalis in his specimens. He obtained a ratio wt. temporalis/wt. masseter=1:1.23 in the juvenile, 1:1.07 in an adult female, and 1:0.9 in an adult male. This indicates that even if the masseter enlarges with age and sex, its growth rate is less than that of the temporalis. The masseter of *Mycetes fuscus* (=*Alouatta fusca*) described by Sirena (1871) presents no significant difference.

Nerve supply: A branch of the anterior division of the mandibular nerve.

Function: Both parts are elevators of the mandible. Pars superficialis and fibers from the anterior three-fourths of the profunda are protractors, those of the posterior deep fourth retractors.

M. pterygoideus lateralis: This two-bellied muscle is found between the anterolateral surface of the medial pterygoid behind and the terminal portion of m. temporalis in front (fig. 3). It is cone-shaped, its base corresponding to the medial wall of the infratemporal fossa and its apex to the processus condyloideus of the mandible. The caput superior is smaller and weaker; its fleshy fibers arise from the facies and crista infratemporalis of the alisphenoid. They pass laterodorsally in an almost horizontal plane to join those of the lower head. The large caput inferior originates by equally fleshy bundles from the lateral surface of the entire pterygoid plate and the perpendicular lamina of the palatine. The bundles also run dorsad but

with increasingly cranial inclination as their origin becomes more caudal. The muscle narrows toward its insertion on the fovea pterygoidea of the condyloid process (fig. 2) and the capsule of the temporomandibular joint. Through the last attachment it is also anchored to the meniscus. The buccal nerve and associated vessels pass forward between both heads. They enter the cheek region after traveling between the lateral pterygoid and temporalis. The observations of Sirena (1871) and Starck (1933) on the same muscle of the howler call for no special comment.

Nerve supply: The buccal nerve innervates the muscle when passing between its two heads.

Function: Protractor of the mandible.

M. pterygoideus medialis: This large muscle is shaped like a frontally compressed cone whose truncated apex corresponds to the pterygoid origin and its base to the ending on the inner surface of the angle and ramus of the mandible (figs. 3, 4). Origin (fig. 5) is (1) by

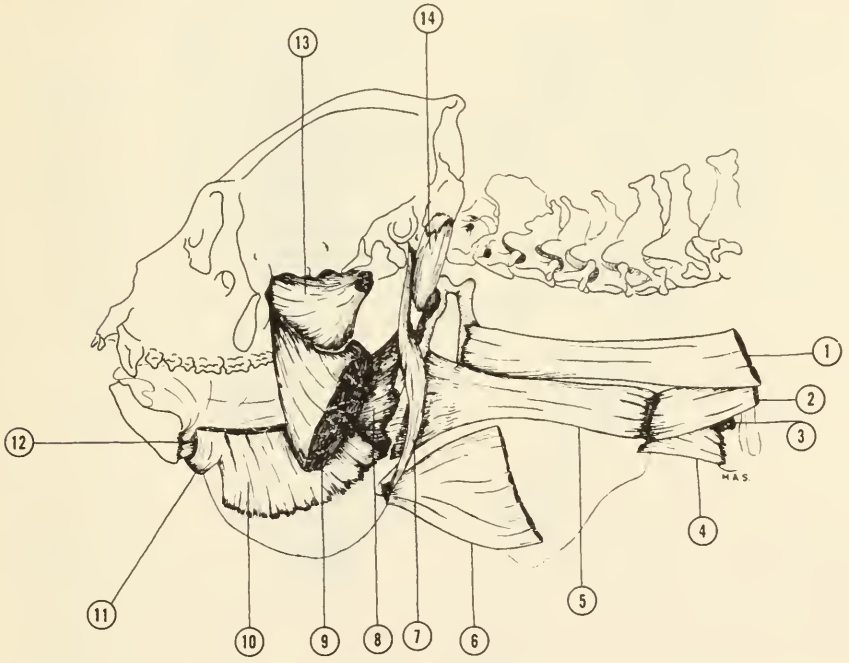

FIGURE 3.—Infra- and Suprahyoid muscles. Some masticatory muscles (1, m. costothyroideus; 2, m. sternothyroideus; 3, m. cricothyroideus, pars obliqua; 4, m. cricothyroideus, pars recta; 5, m. thyrohyoideus; 6, m. sternohyoideus; 7, m. stylohyoideus; 8, m. hyoglossus; 9, m. pterygoideus medialis; 10, m. mylohyoideus; 11, anterior fibers of the mylohyoideus crossing in front of the bulla; 12, genial muscles arising below the torus; 13, m. pterygoideus lateralis; 14, m. digastricus, venter posterior).

fleshy bundles from the inner aspect of the outer and only wing of the pterygoid process below the level of the hamulus, (2) by tendinous fascicles from the pyramid of the palatine bone which form a long and shiny fibrous lamina in the posteromedial surface of the muscle reaching halfway between origin and insertion, and (3) from the

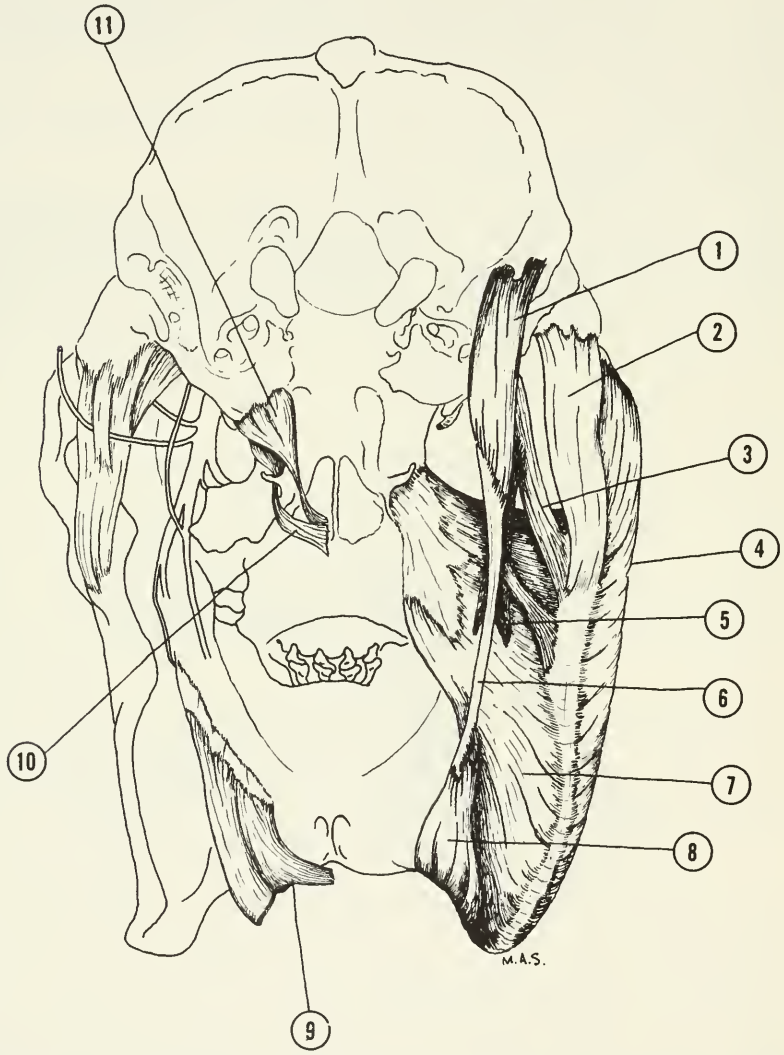

FIGURE 4.—Rear view of the cranium (1, m. digastricus, venter posterior; 2, temporomandibular capsule; 3, lig. stylomandibulare; 4, m. masseter; 5, m. stylohyoideus; 6, intermediate tendon; 7, m. pterygoideus medialis; 8, m. digastricus, venter anterior; 9, m. mylohyoideus; 10, m. tensor veli palatini; 11, m. levator veli palatini).

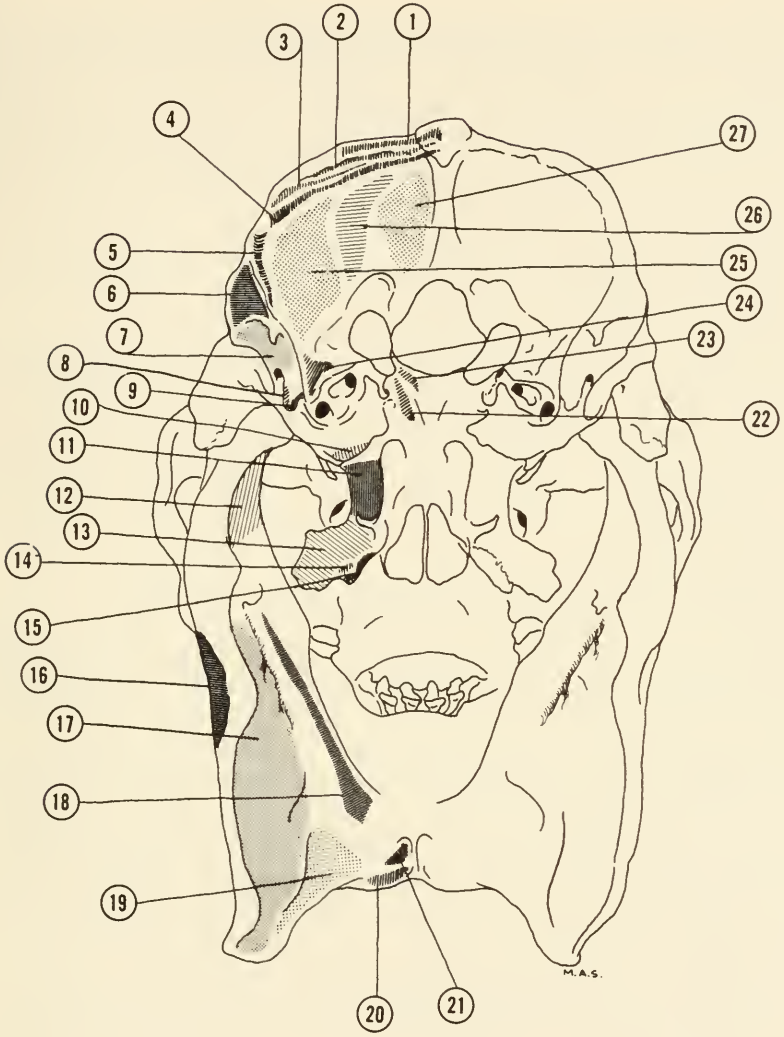

FIGURE 5.—Muscular attachments in the cranium, dorsal view (1, m. trapezius; 2, m. rhomboideus; 3, m. splenius; 4, mm. spinalis et semispinalis capitis; 5, m. longissimus cervicis et capitis; 6, m. sternocleidomastoideus; 7, m. digastricus; 8, m. stylohyoideus; 9, m. stylopharyngeus; 10, m. levator veli palatini; 11, m. tensor veli palatini; 12, m. pterygoideus lateralis; 13, m. pterygoideus medialis; 14, m. palatopharyngeus; 15, m. constrictor pharyngis superior; 16, m. masseter; 17, m. pterygoideus medialis; 18, m. mylohyoideus; 19, m. digastricus; 20, m. geniohyoideus; 21, m. genioglossus, 22, m. longus capitis; 23, m. rectus capitis anterior; 24, m. rectus capitis lateralis; 25, m. obliquus capitis superioris; 26, m. rectus capitis posterior major; 27, m. rectus capitis posterior minor).

posterior and lower borders of the pterygoid wing and more orally from the inferior of the palatine pyramid. Some fibers of the muscle actually override these edges and appear in the infratemporal fossa. Insertion is by both fleshy and tendinous components on the deep surface of the angle and ramus (fig. 2) over a wide quadrilateral area bound below by the basis mandibulae, behind by the dorsal margin of the ramus, and in front by the digastric fossa, the mylohoid, and associated sulcus for the nerve. The upper limit lies at a certain distance from the fossa for the lateral pterygoid. One to three bony ridges of variable development are present within the area and correspond to the attachment of a like number of intramuscular tendinous strands. This description agrees with those of other authors who studied the muscle in this genus (Sirena, 1871; Starck, 1933). Starck (1933), in addition, found it to be divided into a lateral and a medial larger part. Fibers of the first were said to be less oblique.

Nerve supply: A small branch is given off to both the medial pterygoid and tensor veli palatini from the undivided mandibular nerve.

Function: Elevator and protractor of the mandible.

M. tensor veli palatini: This muscle is formed by two triangular portions, a pars descendens and a pars horizontalis united at their respective apices by an intermediate tendon (fig. 4). Pars descendens has a firm origin by means of initially tendinous fibers from the anterolateral aspect of the auditory tube and by fleshy elements from the inner surface of the pterygoid ala, between the hamulus and the base, in front of the foramen ovale (fig. 5). Tubal fibers pass down and forward, those from alar origin are almost vertical. They all converge into a tendon which curves around the hook of the pterygoid. Its fibers spread out within the soft palate to form the pars horizontalis. This meets in the midline with that of the tensor of the other side and contributes to the frame of the palatine aponeurosis. Pars descendens is laterally related to the pterygoideus lateralis from which it is separated by the otic ganglion and the maxillary artery with some of its branches. Medially, it is separated from the levator veli palatini and pharyngeal muscular coat by the highest fibers of the buccopharyngeal fascia. This is reinforced by strong arciform fibers extended between the sphenoid spine and the hamulus.

Nerve supply: The same branch that innervates the medial pterygoid muscle.

Function: It tenses the soft palate.

M. digastricus: The muscle has two well developed bellies connected by an intermediate tendon. It extends from the mastoid region to the inner surface of the mandible. Origin of the posterior belly is by mixed fleshy and tendinous fibers firmly attached to the digastric

area of the mastoid region (figs. 3, 4, 5), which is described in relation to the sternocleidomastoid. The elongated belly is found posterior to m. stylohyoideus and lig. stylomandibulare. Its girth reduces gradually as the muscular bundles end on the lateral surface of the intermediate tendon. This pierces the stylohyoideus deep to the mandibular angle. There are no aponeurotic structures connecting the tendon to the hyoid bone. The fibers of the anterior belly are a continuation of those of the tendon and form a laterally compressed, rather large and fan-like belly whose fascicles are attached to the inner surface of the mandibular ramus and corpus (fig. 2). They mark a shallow but broad triangular fossa in the bone which is limited behind by the insertion of the pterygoideus medialis, above by the mylohoid line, and below by the basis mandibulae. The anterior belly is located between the expanded hyoid body lined here by m. mylohyoideus and the mandible. Sirena (1871) points out that the anterior belly ends on the inner mandibular surface at the junction of the angle with the ramus and without reaching the symphysis. Sandifort (1834) describes a similar attachment in three specimens of *Mycetes* (=*Alouatta*) *seniculus*. Leche (1912) indicates that this insertion does not reach forward beyond the level of the second molar and corresponds behind with the line of the coronoid process. Starck (1933) noted that this ending of the digastricus in a young red howler extends further back and coincides with the lower border of the medial pterygoid. Van den Broek (1920) also says that the digastric area reaches below that of the pterygoid in another young specimen that he examined. The exception to these claims for a peculiar location of the digastric insertion is Bijvoet (1908), who asserts that in the howling monkey this attachment occurs from the level of the masseter to the mental symphysis. It would thus be no different from the pattern in other monkeys (see Leche, 1912).

Nerve supply: A small branch of the postauricular division of the facial nerve reaches the posterior belly. The anterior is innervated by the mylohoid nerve.

Function: Depressor and retractor of the mandible. Tension of the intermediate tendon should help the stylohyoideus in bringing about more effectively the tilting backward of the hyoid bulla as proposed by Schön (1964a).

M. mylohyoideus: This is a broad quadrilateral muscular layer joining the inner surface of the corpus mandibulae to the hyoid bulla. The development of the latter has crowded the muscle into a narrow space between the two bones. Origin is by a fine aponeurotic lamina on the mylohoid line (fig. 2). Rostral fibers arise as close to the mandibular torus (see Scott, 1963, for definition of this term) as 0.5 cm., hinder ones come from very near the mandibular foramen

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and lingula. The muscular bundles are continuations of the rather short aponeurotic fascicles. Insertion is on the lateral surface of the bulla along a line which follows the nonlingual border of the geniohyoideal area of attachment (fig. 3). Anterior fibers of the muscle pass from one mylohyoid line to the other in front of the rostral end of the bulla. Their continuity with the rest of the muscle is not very clear and Sirena (1871) described them as a separate structure, m. transversus maxillae inferioris. On the basis of their origin and topographical relations I regard them as the anterior part of the mylohyoideus which has been partially separated from the rest of the muscle by the changes in the hyoid apparatus. I did not find the continuity of the mylo- and geniohyoideus mentioned by Sirena (1871). The two muscles are indeed very close to each other at the rostral pole of the hyoid, but a space can be demonstrated in between. Sandifort (1834) described the mylohyoideus as thin and embracing the bulla. Bijvoet (1908) also found fibers of the muscle intercrossing in the midline.

Nerve supply: The innervation of the muscle is by the mylohyoid branch of the inferior alveolar nerve.

Function: Elevation of the bulla. It also perhaps collaborates with the geniohyoideus in pulling this bone forward.

Comparative anatomy of the trigeminal group.—Starck (1933) has already pointed out that among the platyrrhines he examined *Alouatta* and *Lagothrix* stand out by themselves with respect to the characteristics of their masticatory muscles. The development of the hyolaryngeal apparatus in the first has influenced these structures and most authors concerned agree on this point (Bijvoet, 1908; Leche, 1912; Starck, 1933). In addition to the overall differences in dimensions it is perhaps those related to the insertion of the anterior digastric belly which is more typical of the howler. The available literature (Bijvoet, 1908; Leche, 1912; Starck, 1933) almost as a whole notes this divergence, which is even more evident in the young individuals (van den Broek, 1920; Starck, 1933). The distorted mylohyoideus is also unique in this animal. *Lagothrix* is peculiar in the orientation of the single-bellied pterygoideus lateralis; the muscle is frontally placed in the infratemporal fossa (Starck, 1933). The differences in the masticatory muscles between the capuchin, spider, and woolly monkeys are minor to the point that Starck (1933) grouped the first two into a single class which did not include *Lagothrix* because of its peculiar lateral pterygoid. The muscles in *Cebus* appear to be proportionately stronger than in the Atelinae and the fascicles of the masseter reach the inner surface of the angle by turning around the basis mandibulae (Starck, 1933). A zygomaticomandibular portion was very strong in one of the capuchin specimens of Starck (1933),

who also points out that the development of a strong temporalis contributes to the occasional formation of a sagittal crest in *Cebus*. The pterygoideus lateralis of *Ateles* (Starck, 1933) appears to be small. All these muscles in *Brachyteles* (Hill, 1962) have a strong resemblance to those of the spider monkey. Hill (1962) claims the presence of a zygomaticomandibularis in the woolly spider monkey.

Facial Group

Huber (1930, 1931, 1933) classified the muscles in the field of m. facialis into a superficial and a deep group. The first comprises all the muscles discussed under facial musculature; the second includes the stylohyoideus, posterior digastric belly, and the stapedius muscle. The little muscle to the stapes was not exposed in my dissections, and the whole of the digastricus was studied with the masticatory muscles for functional reasons.

Facial Musculature

The facial musculature of some representative ceboids was the object of an excellent study by Schreiber (1928). He examined four specimens of *Alouatta auratus* (=*Alouatta seniculus*), two adult males, one adult female, and one infantile whose sex was not specified. My investigation corroborates and in some aspects complements his findings for this genus. Van den Broek (1920) describes some of these muscles in a young *Mycetes* (=*Alouatta sp.*) with full milk dentition. Huber (1930) refers to some of the intrinsic ear muscles in the Central American species *Alouatta palliata*. Ruge (1887) does not say how many specimens of *Mycetes* (=*Alouatta sp.*) he used, but his results are largely confirmed by Schreiber (1928). Sirena's account (1871) uses a different nomenclature but his material is comparable with those of other authors and my own. He gives no information about the intrinsic ear muscles.

Material for this section was obtained from four specimens. The whole facial musculature could be studied in but two males; the other male and the female provided partial information.

M. platysma colli et faciei: This is a well developed but thin muscular sheet which covers the posterior and most of the anterior cervical triangles, the parotideomasseteric, and part of the buccal and mental regions (fig. 6). Its fleshy fibers arise freely in the superficial fascia of the neck along a line that follows first the clavicle and then, up toward the ear, the dorsal border of the posterior cervical triangle. Some fibers override mm. trapezius and the atlantoscapularis anterior extending dorsally for a very short distance but never all the way to the back of the neck. Only Hill (1962) describes the origin of the muscle as almost reaching the dorsal midline in the nape, an observation which I regard as his own because it is not found in any of the authors on whose

works his is said to be partially based. The anteromedial bundles of the platysma converge toward the symphyseal region of the mandible. Lateral fascicles pass horizontally across the lateral aspect of the face right below the ear and zygomatic arch to reach the angle of the mouth. Those in between have an intermediate direction. The clavicular and lower cervical fibers insert (1) on the basis mandibulae and higher up, along a line which corresponds with the reflection of the oral mucosa, on (2) the corpus from the juga alveoraria to the level of the first or second molar. A few of them enter the lower lip superficial to m. orbicularis oris and end about 1 cm. from the oral aperture. The platysma fibers attaching in relation to the incisors are more abundant and the muscle looks stronger here. Schreiber (1928) said that some of them

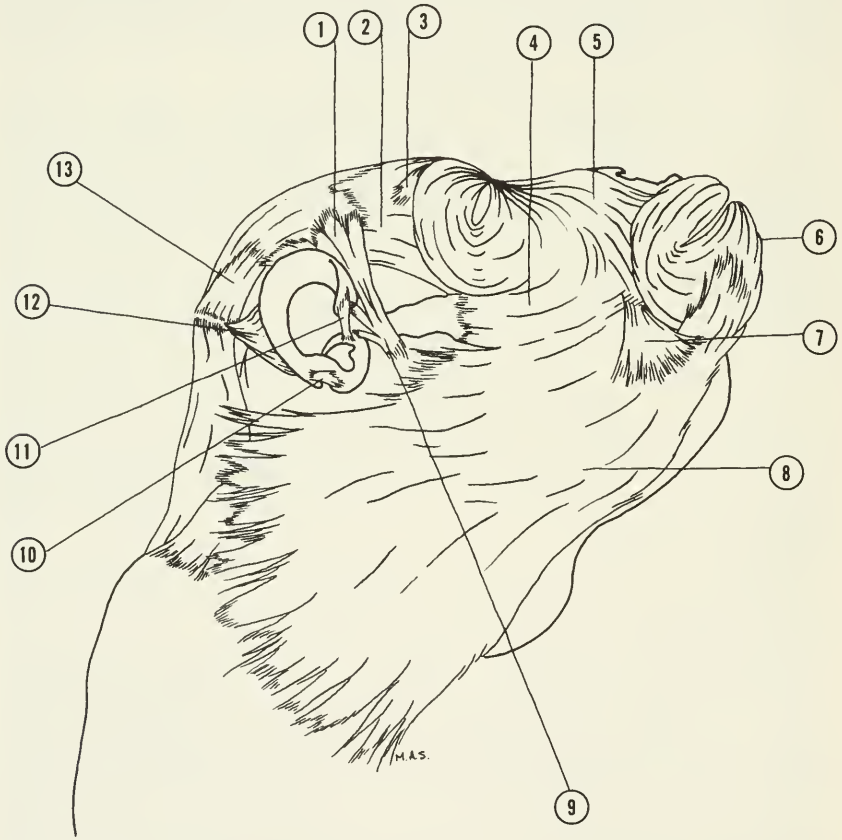

FIGURE 6.—Facial musculature (1, m. auricularis anterior et superior; 2, mm. frontalis and orbito-auricularis; 3, m. corrugator supercilii; 4, zygomatico-orbital plate; 5, m. nasolabialis; 6, m. orbicularis oris; 7, m. triangularis; 8, m. platysma colli et faciei; 9, m. depressor helicis; 10, m. antitragicus; 11, m. tragohelicinus; 12, m. auricularis posterior; 13, m. occipitalis).

actually originate on the basis mandibulae and join the rest to end on the corpus. The ventromedial margin of the platysma is well defined, except for some aberrant fibers which in the submental triangle intercross with equally aberrant fascicles of the opposite side muscle. The bundles directed toward the angle of the mouth run between the orbicularis oris and buccinator under cover of a variably developed m. triangularis. They end by intermixing with the fascicles of the orbicular and buccinator. The fibers of the upper border of the muscle form a continuous lamina with those of the zygomatico-orbital plate in the zygomatic region and forward. They pick a few additional bundles (m. auriculo-labialis inferior of Ruge, 1887) from the region of the incisura anterior (auris). Ruge (1887) and Schreiber (1928) described similar fibers in *Alouatta*, but the latter author did not find them in one female and a very young specimen. The clavipectoral fascicles of the platysma from each side advance toward the mental region. They approach and eventually reach the midline. The thyroid prominence, part of the hyoid bulla, and the anterior poles of the submandibular glands are seen in the area thus bound by the muscles. I could not verify the distal double layering described by Schreiber (1928) in all his adult specimens. M. platysma is innervated by branches of the lower buccal rami of the facial nerve.

M. occipitalis: It is a quadrilateral lamina whose fleshy fibers arise from the protuberantia occipitalis externa and a little more than the medial half of the lambdoid crest (fig. 6). They all run forward to end on the dorsal border of the galea aponeurotica after covering approximately the rear third of the cranial vault. The muscle is paired. The two flat bellies, lying at each side of the midline, are separated by a wedge-shaped and backward-pointing expansion of the galea which thus reaches the protuberance. Its origin is partially covered by the auricularis posterior, and the dorsal fibers of the auricularis anterior et superior are seen over its lateral margin.

M. auricularis posterior: It retains a connection with the occipitalis, but neither of them has any with m. platysma colli et faciei (fig. 6). Origin is from the lateral half of the lambdoid crest up to the point where this turns downward. The fleshy fibers of the muscle spread out laterally forming four or five slips whose attachment is on the eminentia conchae. These bundles were continuous in the right side of one male with the mm. obliqui et transversi.

Nerve supply: The postauriculo-occipital muscles are all supplied by the ramus auricularis posterior of the facial nerve.

Mm. obliqui et transversi (m. auriculae proprius posterior of Ruge (1887) and m. auricularis proprius of Schreiber (1928)): They appear as transversely oriented strands joining the eminences of the scapha and concha all along the fossa anthelicis.

M. antitragicus: It corresponds to the lower fibers of the former (Huber, 1933), which can be seen on the outer surface of the auricle connecting the antitragus and the cauda helicis across the fissura antitragohelicina (fig. 6).

M. helicis: It is a slender small band under cover of the tragohelicinus. Origin is on the spina helicis and insertion on the crus helicis. Contrary to Schreiber (1928) I did not find it to be strong.

Nerve supply: The innervation of the previous three intrinsic ear muscles is also provided by the ramus auricularis posterior n. facialis. They, and other auricular muscles as well, are of variable development.

In agreement with Hill (1962), Huber (1931), and Schreiber (1928) I found no trace of the sphincter colli profundus, but the following muscles which are all derivatives of this matrix layer (see Huber, 1930, 1931, 1933) were observed to be well developed, if not highly differentiated. They are all supplied by the preauricular rami of cranial nerve VII.

M. auricularis anterior et superior: It arises from the anterosuperior part of the convex surface of the auricle. The fibers radiate upward between the skin and the galea aponeurotica, to end more or less associated with the last structure (fig. 6). The muscle is innervated by both the ramus auricularis posterior and the rami auriculares of the auriculo-temporofrontal branch of the facial.

M. frontalis: It forms a thin fleshy lamina between the anterior border of the galea aponeurotica and the superciliary arch from where it arises under cover of both the corrugator supercilii and the pars orbitalis of the zygomatico-orbital plate (fig. 6). Laterally its fibers form a single continuous layer with those of the next muscle to be described, medially the frontalis of each side touch each other.

M. orbito-auricular: This plate is made of fascicles of similar appearance and direction to those of m. frontalis. They extend from the anterior border of the galea, in front of the auricle, to the processus zygomaticus of the frontal bone (fig. 6). Its bony anchorage is covered by both pars orbitalis and zygomatica of the zygomatico-orbital plate. The galeo-orbito-auricular junction lies under the anterior fibers of m. auricularis anterior et superior.

M. tragohelicinus: It is a flattened muscular column between the tragus and the beginning of the helix (fig. 6).

M. depressor helicis: It is different in each of the males. In one it is formed by two separate bundles which, arising from the spine of the helix and tragus, converge in front of the auricle where they are joined by fibers descending from the anterior border of the m. auricularis anterior et superior (fig. 6). Ending is on the subcutaneous fascia of the face over the temporomandibular joint and parotid gland. In the

other specimen the muscle is a thin fascicle with origin on the anterior part of the helix. Descending in the subcutaneous preauricular fascia it ends in front of the ear cartilage. Schreiber (1928) found three different arrangements for this muscle, but none of them was similar to either of those I have described.

M. zygomatico-orbital: This muscular mass is an extensive and well-developed sheet lying over the zygomatic, supraorbital, infraorbital, and orbital regions with little differentiation of its two parts (fig. 6): The fibers of pars zygomatica arise from the outer surface of the anterior two-thirds of the jugal arch and run forward as a broad band across the malar bone and the large zygomatico-orbital foramen to reach the infraorbital region. They expand fanwise toward the upper lip and nose where they end (1) by intermixing with those of the orbicularis oris, and (2) under cover of the orally descending fibers of the nasolabialis. This part and the platysma colli et faciei form a single lamina as described before. The bundles of pars orbitalis have origin on the medial palpebral ligament and run laterally forming arcades within both the upper and lower eyelids. Deep fascicles attach to the respective tarsal plates, superficial ones end on the skin. The longest reach the lateral palpebral commissure. Two zones can be recognized in pars orbitalis: one occupies only the lids, the other is thicker and formed by the more peripheral bundles.

M. depressor supercilii could not be demonstrated.

M. corrugator supercilii: It is composed of a few fibers and lies in the supraorbital region between the pars orbitalis of the zygomatico-orbital plate and the frontalis (fig. 6). Origin is on the glabella and its fascicles spread laterally along the superciliary arch to end by intermixing with those of the pars orbitalis and in the skin of the region.

M. nasolabialis: It forms a muscular sheet extending from as high as the interorbital space, over the root of the nose, to the infraorbital and oral regions (fig. 6). Origin is from the skin of the glabella and insertion takes place by intercrossing with m. orbicularis oris. The muscles of each side are continuous without interruption over the midline. Schreiber (1928) calls it m. levator labii alaeque nasi and describes some of its fibers as passing upward covering m. frontalis (his m. orbitotemporo-auricularis). They perhaps correspond to m. corrugator supercilii.

M. maxillo-nasolabialis: It appears as a well differentiated but rather weak slip extended from the maxilla to the upper lip across the infraorbital region where it lies under the zygomatico-orbital mass (fig. 1). Origin of its fleshy fibers is from the alveolar border of the maxilla above the premolars and the attachment of the buccinator (pars maxillaris). They pass over the infraorbital vessels, the nerve

and the caninus part of the caninus-triangularis complex. The fascicles radiate out toward the mouth and nose, the anterior ones (pars labialis) reaching the upper lip where they end by intermixing with the orbicularis oris, the more posterior (pars nasalis) on the fascia deep to the nasolabialis around the apertura piriformis and the dorsum of the nose. In one male the pars nasalis and pars labialis on both sides of the face were individually discrete bands separated by a hiatus. The muscle is a common feature among known platyrrhines (Schreiber, 1928).

M. orbicularis oris: It is formed by abundant muscular bundles of variable length which pass from the labial skin to the mucosa and vice versa, surrounding the oral aperture (fig. 1). A rather broad lamina is thus formed within the lips, thinner in the upper where it occupies the space between the free border and the piriform opening, thicker in the lower and filling the whole lip.

M. caninus: This is a triangular and strong sheet extended from the paranasal to the oral region across the infraorbital (fig. 1). It lies deep to the maxillonasolabialis and to the infraorbital vessels and nerve. Origin is from along the naso- and premaxillomaxillary sutures. Its fibers run down and laterally toward the upper lip and the angle of the mouth; the more anterior follow the same direction as those of the orbicular with which they seem to form a single muscular layer.

M. triangularis: It has a variable development (fig. 6). In two males it is formed by many fibers which are continuations of the caninus. They become superficial near the angulus oris by passing stepwise through those of the zygomatico-orbitalis-platysma complex. Their ending is on the skin of the region with the anterior fibers following the direction of the orbicularis and the posterior ones diverging at an angle from the corner of the mouth. In the other male the triangularis was not present as a superficial structure and in the female the muscle was rather weak. Ruge (1887) says it is absent in *Mycetes* (=*Alouatta sp.*).

M. buccinator: In agreement with Schreiber (1928) and contrariwise to Ruge (1887), I found this structure a complicated arrangement. The well developed muscle lies in the buccal region covered by m. platysma and the zygomaticoorbital plare. It is organized in three layers each with different fiber direction (fig. 1): (1) Superficial bundles are present only in the oral half of buccinator where they form a laterally compressed belly of variable development and even in the same individual its magnitude may be different bilaterally. Typically, these fascicles run from the alveolar border of the maxilla to that of the mandible following a vertical and rostrally concave path. They are separated from the orbicularis oris by the platysma-zygomaticoorbital complex and appear to be a part of the first muscle after re-

moval of the last two. (2) Fibers of the intermediate layer arise from the outer edge of the maxillary alveolar border and the ill-defined pterygomandibular raphe. Running almost horizontally forward they end deep to the orbicularis intermixing with other buccinator fibers at the angulus oris. (3) The deeper stratum can be seen between the mandible and the lower margin of layer (2). Origin is from the said raphe, the lower part of the temporal crest of the mandible, and the external border of the alveolar process. Its fibers run obliquely toward the corner of the mouth at an angle to those of the previous layer. They have a similar ending. I could not demonstrate a double layering of fibers in layer (3) as claimed by Schreiber (1928). The whole muscle is separated from the overlying ones by the clumps of an extensive facial fatty pad. Sirena (1871) and van den Broek (1920) describe, in no very clear details, a paired m. mentalis. I think that both might have been confused by the deep fibers of the platysma inserted on the juga alveolaria. Schreiber (1928) does not include the mentalis in his account of the howler, but adds when discussing this muscle among the platyrrhines that the condition in the hapalids (=callithricids), that is, the presence of a mentalis, is a character common to the other species he studied. I could not demonstrate this muscle.

Nerve supply: All the derivatives of the sphincter colli profundus are supplied by branches of the preauricular rami of the facial nerve.

Comparative anatomy of the facial musculature.—Huber (1930) regarded as progressive the common features of the facial musculature which are found in the howling, spider, and woolly monkeys. These characters have also been observed by other authors in *Ateles* (Hill, 1962; Schreiber, 1928), *Brachyteles* (Hill, 1962), and *Lagothrix* (Hill, 1962; Schreiber, 1928).

Cebus contrasts with the Atelinae and *Alouatta* in possessing a less differentiated platysma and clear remains of an m. sphincter colli profundus. The platysma colli et faciei in this genus arises from the nuchal ligament where it is partially covered by the suboccipital origin of m. auricularis posterior and the occipitalis (Schön, 1964b). It has no insertion on the basis mandibulae and no connection with the zygomatico-orbital plate (Ruge, 1887; Schreiber, 1928). A variably developed m. sphincter colli profundus was observed by Schreiber (1928) in three adult males, one *Cebus macrocephalus* (=*Cebus apella*), one *Cebus capucinus*, and one *Cebus variegatus* (=*Cebus apella*). I saw this muscle in one adult male *Cebus nigrivittatus*. M. triangularis appears as a derivative of the orbicularis oris because the caninus is small (Schreiber, 1928).

The platysma colli et faciei of *Alouatta* differs from that of *Ateles* and *Lagothrix* in the fact that it is more extensive over the face where it forms a continuous sheet with the zygomatic-orbital plate. The

spider and the woolly monkey resemble *Cebus* in the separation of these two muscles across the face and in the absence of insertion to the basis mandibulae. I regard the condition in the howler as a specialization. The factors responsible for such a change are perhaps the same that caused the enormous enlargement of the mandibular ramus. Leche (1912) correlated the modifications in the whole skull of *Alouatta* with the expansion of the hyoid bulla and associated structures. More recently, Biegert (1963) arrived at the same conclusion. I think that what affected the mandible was also operating over the whole lateral aspect of the face, influencing its several structures in different degrees (see muscles of the trigeminal group). The platysma colli et faciei of the howler was therefore modified and underwent an expansion to the point of becoming fused with the pars zygomatica of the zygomatico-orbital plate. This widening may perhaps have caused also the variable condition of m. triangularis in *Alouatta*. Sirena (1871) apparently did not find this last muscle. Ruge (1887) indicated its absence in the genus. Schreiber (1928) says that it is present and in a larger condition than in *Ateles* and *Lagothrix* in which it seems to be a constant feature. Hill (1962) declares it to be a stout structure in *Brachyteles*, and *Cebus* has a large one (Ruge, 1887; Schreiber, 1928). The situation in the howler with respect to this muscle could be taken to indicate that its presence as a superficial structure is a morphological feature which has not attained yet a fixed pattern due to the change suffered by m. platysma colli et faciei. This broadening resembles to a certain degree what is known about *Brachyteles* (Hill, 1962), a genus where the mandibular ramus is also fairly large. Following Hill's description of this bone in *Alouatta*, *Brachyteles*, *Lagothrix*, and *Ateles*, their mandibles can be arranged in this decreasing order according to the size of the ramus. The howler and the woolly spider monkey with larger platysma colli et faciei are at the top. The insertion of this last muscle on the mandibular basis of *Alouatta* (Ruge, 1887; Schreiber, 1928; this study) and its absence in *Ateles* (Ruge, 1887; Schreiber, 1928) and *Cebus* (Ruge, 1887; Schreiber, 1928) is perhaps an adaptation of the platysma for its function of helping hold in place the large hyolaryngeal structures which it covers at each side of the neck. Ruge (1887) describes in *Lagothrix* an attachment of the platysma to the basis, but Schreiber (1928) says there is none. No information respecting *Brachyteles* is available.

Deep musculature

A description of the styloid region in *Alouatta* is necessary in order to have a clearer view of the muscles arising from this part of the cranium. The area lies in the outer third of the posteroinferior surface of the petrous bone, between the stylomastoid foramen laterally and

the large irregular fossa for the jugular and carotid foramen medially. It is traversed from behind forward by the horizontal ramus of the postmastoid crest (see description of the mastoid zone with sternocleidomastoid muscle and fig. 9) as this passes orally just lateral to the vascular openings. This extension of the crest forms the lateral and well defined margin of the carotideo-jugular fossa and is quite sharp in relation to the arterial foramen where it gives rise to the stylomandibular ligament. Midway between the venous and arterial apertures a laterally directed and irregular ridge branches off toward the exit of n. facialis. It corresponds in young specimens to the junction of the anulus tympanicus with the mastoid zone of pars petrosa. Its development is variable in adults where we have seen it often replaced by just a short knob. It gives rise to the styloid muscles and together with the part of the crest around and in front of the carotid opening corresponds to the petrous crest of Zukerman, Ashton, and Pearson (1962).

M. stylohyoideus: A long, well-developed muscle which connects the anteroinferior aspect of the petrous bone to the hypohyale (Schön, 1964a; Sirena, 1871). Origin is from the lateral half of the petrous crest where short tendinous fibers form a flat and broad band. Its continuing fleshy belly is penetrated from behind and below by the intermediate tendon of the digastric upon which some of its fibers are directly inserted. The rest of the muscle attaches to the hypohyale as a fine tendon. In both sides of the female the medial bundles are continuous with those of the mylohyoideus.

Nerve supply: A small branch of the postauricular division of the facial nerve.

Function: The possible importance of this muscle in relation to the howling mechanism was previously reported (Schön, 1964a). It should suffice here to say that the contraction of the stylohyoideus would tilt the hyoid bulla back and upward. By this movement the hyolaryngeal canal can be closed, as it is then pressed between the epiglottis and the receding hyoid.

Glossopharyngeal Group

M. stylopharyngeus: This strong and well differentiated muscle arises by fleshy fibers from the lateral half of the petrous crest (see description of this bony landmark in relation with the styloid region) between the origin of m. stylohyoideus and the carotid foramen (fig. 5). Its round belly lies against the upper pharyngeal constrictor and the pharyngobasilar membrane, both of which are lined by the buccopharyngeal fascia. The stylopharyngeus runs downward and medially to enter the pharynx through the middle pharyngeal hiatus together with cranial nerve IX. Its fibers spread out now as an in-

creasingly wider band along the walls of the larnygopharynx (fig. 7). They lie between the two lower constrictors and the palatopharyngeus. Lateral bundles descend to the distal part of the thyroid lamina and lesser horn on whose posterior borders they insert. I failed to clearly demonstrate this attachment in a previous work (Schön, 1964a) and, therefore, is described here. The stylopharyngeal fibers then said to end on the mucosa of the laryngeal saccules are now regarded as belonging to the middle pharyngeal constrictor. Medial and intermediate fascicles end on the fibrous inner fascia of the pharynx. Both

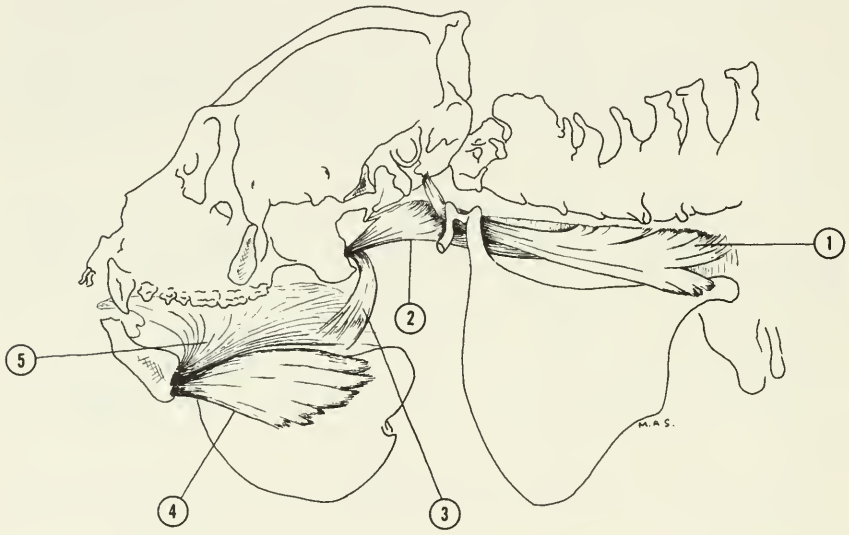

FIGURE 7.—Pharyngeal and lingual muscles (1, m. stylopharyngeus; 2, m. palatopharyngeus; 3, m. palatoglossus; 4, m. geniohyoideus; 5, m. genioglossus).

Lampert (1926) and Sandifort (1834) recognized this muscle as strong in the howler monkey.

Nerve supply: Glossopharyngeal nerve.

Function: Elevation of the larynx and constriction of the laryngopharynx.

COMPARATIVE ANATOMY OF THE GLOSSOPHARYNGEAL GROUP.—Lampert (1926) describes m. stylopharyngeus in *Ateles* as being also powerful and notes its presence in *Lagothrix*, but adds no more details.

Vago-accessory Group

M. constrictor pharyngis superior: It is shaped like a canal open ventrally and has extensive origins from different structures at each side of the midline. (1) A pars pterygopharyngea has its fleshy fascicles arising from the inner surface of the pterygoid process (fig. 5) where

they are attached to a bony prominence formed by the pyramid of the palatine (pars palatopharyngea might be a proper denomination). These fibers swing dorsally toward their insertion on the basilar process of the occipital (fig. 5). They leave a space between the upper border of the constrictor and the base of the skull, the upper pharyngeal hiatus, through which the auditory tube enters the pharnyx. This part was completely absent in one male and appears in the female as shown in figure 8. (2) Pars buccopharyngea follows part (1) and is represented by bundles with origin in the poorly defined ptery-

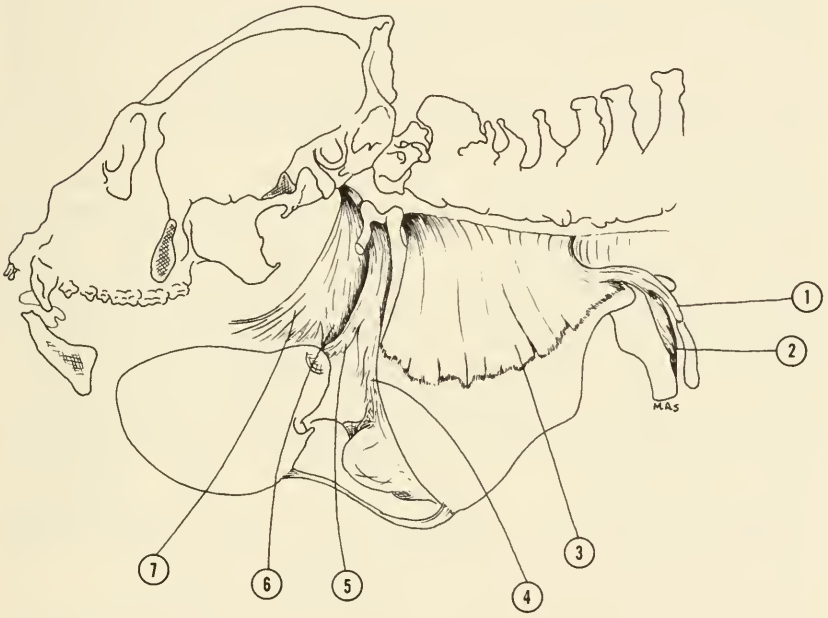

FIGURE 8.—Muscles of the pharynx (1, m. constrictor pharyngis inferior, pars tracheopharyngea; 2, m. constrictor pharyngis inferior, pars cricopharyngea; 3, m. constrictor pharyngis inferior, pars thyropharyngea; 4, m. constrictor pharyngis medius, pars membranacea; 5, m. constrictor pharyngis medius, pars lingualis; 6, m. constrictor pharyngis superior, pars glossopharyngea; 7, m. constrictor pharyngis superior, pars buccopharyngea).

gomandibular raphe and even sometimes in the inner surface of the mandibular ramus (pars mylopharyngea) (fig. 8). As for the pterygopharyngeal fibers, they also run back toward the base of the cranium. (3) Fascicles coming from the sides of the tongue have their origin reaching the tip of this organ in three males (see Schön, 1964a, figs. 2, 3, 4), but reaching only the level of its root in another male and the female (fig. 8). They form pars glossopharyngea and run dorsally to

join the rest of the muscle after receiving the bundles of the styloglossus when this is present. Some of the lingual elements arise from the sides of the hyoglossal membrane adjacent to those of the middle constrictor (fig. 8). The fibers of the superior constrictor previously described as coming from the lateral air sacs (Schön, 1964) are now regarded as belonging to the middle constrictor.

Nerve supply: Branches of the pharyngeal plexus.

Function: Constrictor of the upper pharynx and retractor of the tongue when complete.

M. constrictor pharyngis medius: It is the smallest of all three pharyngeal constrictors and can be well visualized only after ablation of both cornu branchiale I (see Starck and Schneider, 1960, for definition of this term) and the thyroid lamina. Its fibers of origin are arranged into three groups. (1) Pars lingualis originates from the hyoglossal membrane and intrinsic lingual muscles by a mixture of fleshy and fibrous fascicles which are immersed in abundant adipose tissue (fig. 8). They run backward around the root of the tongue to join the rest of the muscle. (2) The greater number of fibers arise within a fatty environment from the membrane of the laryngeal saccules and form the pars membranacea (fig. 8). They are initially covered by the thyroid lamina but further dorsally are found above its cranial border and lined by the thin thyrohyoid membrane. These fascicles cross the epiglottis in a craniodorsal direction and join those of the rest of the muscle under the bicornual articulation. (3) Pars cornualis is represented by a small number of fibers which, arising at the distal end and medial surface of cornu branchiale I, contribute immediately to the formation of the muscle. All fibers of the middle constrictor run dorsally with a slight cranial inclination to end on the midline raphe of the back of the pharynx.

Nerve supply: Branches from the pharyngeal plexus.

Function: Besides its role as a pharyngeal sphincter by the contraction of all its fibers, the muscle can also act in emptying the laryngeal saccules through its pars membranacea. The constrictor effect upon the alimentary canal probably takes place in swallowing simultaneously with the contraction of the levators of the larynx. At this moment the palatopharyngeus and the middle constrictor will contribute to isloate the rhino- from the oro- and laryngopharynx by pressing the walls of the pharynx against the prominent epiglottis.

M. constrictor pharyngis inferior: Four parts can be described in this large muscle according to the different cartilaginous areas from which it arises (fig. 8). (1) Pars thyropharyngea: A great many fleshy fibers come from the lateral surface of the thyroid lamina where they are covered by the costothyroideus and thyrohyoideus. This origin extends from the upper to near the lower margin of the lamina.

There is no trace of a linea obliqua or superior and inferior tubercles. The laminar fascicles are all horizontally directed toward the dorsal midline raphe where they are inserted. (2) Pars cricopharyngea: The distal border of the cricoid arch gives rise to several bundles which, running more or less horizontally backward, reach the level of the cricothyroid articulation. They now change their direction and pass cranially covering the lower horn up to the level of the lower laminar margin. A new change in direction takes place whereby the fascicles join those of the pars thyropharyngea with which they end on the dorsal midline raphe of the pharynx. (3) Pars tracheopharyngea: Fleshy fibers originate from the tip of the first tracheal cartilage and form a muscular band which runs backward along the tracheocricoid junction. It turns cranially around the end of the lower thyroid horn and ascending parallel to the posterior border of the cartillage reaches the level of the lower margin of the lamina. The fascicles now pass horizontally toward the midline raphe, forming a single muscular sheet with those of parts (1) and (2). (4) Pars cornuopharyngea: A small group of fibers arises on the posterior border of the cornu inferius under cover of the ascending portions of the tracheal and cricoid parts which it joins. The cricopharyngeal sphincter is therefore formed by fascicles which from each side of the respiratory canal are first directed dorsally, then ascend to change again their direction and pass dorsomedially toward the back of the pharynx.

Nerve supply: The ramus externus of the n. laryngeus superior is the main contributor to the formation of the pharyngeal plexus which sends several branches to this muscle.

Function: Fibers of pars thyropharyngea are sphincteric to the laryngopharynx. Their constrictor effect over this part of the digestive tube is extended to the laryngeal saccules found between the inner surface of the thyroid lamina and the vestibule of the larynx. Air will be squeezed out of these sacs on contractions of the muscle. By the same mechanism the deep piriform recesses of the pharynx will also be reduced. An interesting function could possibly be ascribed to the cricopharyngeal sphincter on the basis of the direction followed by its fibers. Its contraction could tilt the cricoid cartilage bringing the arch downward and therefore the arytenoids forward. The cornual fibers and the bending of both pars trachealis and cricoidea around the tip of the lower horn ensures that the pulling effect is properly carried. This action should have influence in the production of certain tones as the displacement forward of the arytenoids brings their vocal process closer to the thyroid angle with the consequent relaxation of the vocal folds.

M. palatopharyngeus: It is well developed and contributes in the formation of the lateral and posterior walls of the pharynx. Origin

is by fleshy fibers from (1) both oral and nasal surfaces of the so palate near the attachment of this structure to the pterygoid proces (2) the inner surface of the pyramidal mass of the palatine (fig. 5 and by a few muscular bundles from (3) the medial end of the auditor tube behind the origin of m. levator veli palatini. It descends into th pharynx between the pharyngobasilar fascia and the muscular coat the organ to end by intermingling of its fibers with those of th expanded portion of the stylopharyngeus (fig. 7).

Nerve supply: Could not be determined.

Function: Elevation of the larynx.

M. palatoglossus: The arcus palatoglossus contains this not ver prominent muscle. Its fleshy fibers come from the oral surface of th soft palate and pass downward deep to the mucosa of the isthmu faucium to end on the lateral side of the root of the tongue (fig. 7

Nerve supply: Could not be determined.

Function: Closure of the isthmus.

M. levator veli palatini: It is a smaller muscle than the tensor ve palatini and entirely intrapharyngeal in location. It is shaped lik a transversely compressed pyramid whose apex slants forward an medially. The base corresponds to the origin of the muscle from th posteromedial aspect of the auditory tube and adjacent bony surfac of the petrous bulla (figs. 4, 5). Its fleshy fibers run down, forwar and medially to the soft palate where they end over the nasal surfa of the palatine aponeurosis.

Nerve supply: A small branch of the pharyngeal plexus reach the muscle.

Function: It elevates the soft palate.

The intrinsic muscles of the larynx which also belong in the vag accessory group have been extensively dealt with by several invest gators. Starck and Schneider (1960) present an excellent summary these structures. Kelemen and Sade (1960) were also concerned wit them in their study made with gross microscopic sections of the laryn in three specimens of *Alouatta palliata*. There is little which I cou add at the present to the information afforded by these worker For that reason it has been decided not to include here a descriptio of the intrinsic laryngeal muscles.

M. sternocleidomastoideus: It is a columnar and somewhat laterall compressed muscle extending from the postotic region of the skull t the clavicle and sternal processes (see Schultz, 1961, for definitio of this term). It arises by short tendinous fibers organized into stout bundle from the highest part of the mastoid region. The mastoi zone is triangular (fig. 9). A crest, to which I shall often refer postmastoid, corresponds to the dorsal margin. An irregular tran verse ridge divides the zone into an upper and rough area for th

origin of the sternocleidomastoid, and a lower and deeper one for that of the digastric. The fleshy fibers of the sternocleidomastoid pass caudally, forward, and medially delimiting the anterior and posterior cervical triangles. During its course over the neck the muscle is contained within the investing layer of the cervical fascia which is particularly resistant near the mandible and continuous with the parotid sheath. The distal end of the muscle expands fanwise at the insertion. Its fleshy fibers attach on the upper and posterior aspect of the medial two thirds of the clavicle, the sternoclavicular capsule, and the upper and posterior surfaces of the sternal process. The observations of Sirena (1871) coincide with mine.

Nerve supply: The spinal accessory nerve, together with contributions from C II and III.

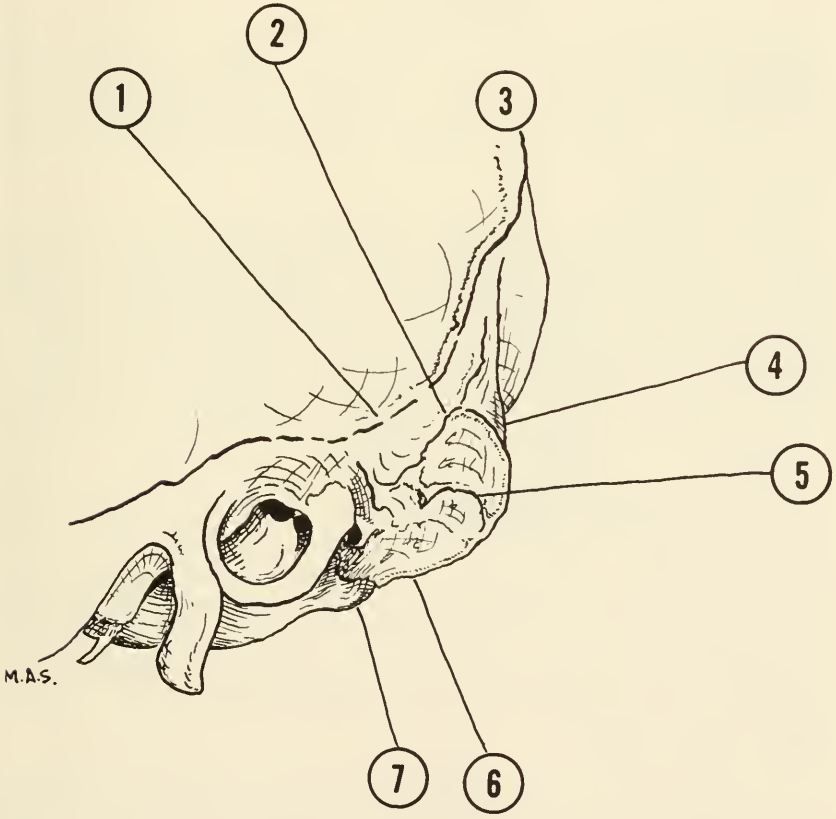

FIGURE 9.—Mastoid and styloid regions (1, supramastoid crest; 2, premastoid crest; 3, horizontal part of lambdoid crest (nuchal line); 4, descending part of the lambdoid crest also called postmastoid crest; 5, separation between the sternocleidomastoid and digastric areas; 6, horizontal ramus of postmastoid crest; 7, styloid region).

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Function: Rotator of the head.

The trapezius will be treated with the muscles of the upper extremity for functional and topographical reasons.

Comparative anatomy of the vago-accessory group.—The findings of Lampert (1926) in the three pharyngeal constrictors of a male *Mycetes auratus* (=*Alouatta seniculus*) and a female *Mycetes belzebuth* (=*Alouatta belzebul*) are like those I described. Sandifort (1834) noted the strong development of the constrictor musculature of the pharynx, particularly the part attached to the thyroid cartilage. The three constrictors in *Ateles*, *Cebus*, and *Lagothrix* (Lampert, 1926) are comparable to those of the howler but smaller, in harmony with the lack of enlargement of the larynx and the hyoid. Both *Cebus* and *Ateles* have an m. intercornualis (Lampert, 1926).

Extraocular Group

There are only seven muscles concerned with the motility of the eyeball in *Alouatta*, namely, a m. levator palpebrae superioris, two obliqui and four recti (fig. 10). In agreement with Ottley (1879), who says that a m. retractor bulbi is absent in platyrrhines, I did not find it in the howler. Sirena (1871) states that these muscles agree with those of man.

M. levator palpebrae superioris: This muscle arises from the upper margin of the optic foramen above the attachment of the common tendon and lateral to the origin of the superior oblique. Its fleshy fibers pass forward as an initially small stalk, but soon fan out into a thin muscular layer which enters the upper lid and ends within its substance. The muscle lies between the periorbita and the rectus superior. A branch of the oculomotor nerve penetrates its deep surface to supply it.

M. obliquus superior: Origin is by fleshy fibers from the upper root of the alisphenoid, medial to the previous muscle and above the common tendon. It forms a round, long belly which runs forward along the medial orbital wall above the rectus medialis. This reaches the pulley where the muscle thins down into a round tendon which turns laterally between the rectus superior and the eyeball. Insertion takes place behind the equator in the posterolateral quadrant. N. trochlearis enters the lateral surface of the superior oblique near the origin of the muscle.

M. rectus superior: It arises by the anulus tendineus communis through which its fibers are attached to the upper margin of the optic foramen below the origin of m. levator palpebrae superioris. It runs forward and is inserted as a thin membrane into the sclera, about one-quarter or one-third of the way between the equator and the corneoscleral junction. The main axis of this muscle forms an acute angle

with that of the superior oblique tendon. This condition was already described by Ottley (1879) for the Cebidae. It is innervated by the upper branch of the oculomotor nerve.

M. rectus lateralis: Origin from the orbito- and alisphenoid where its fascicles of origin constitute the lateral part of the common tendinous ring. The continuing fleshy fibers form a laterally compressed and large belly which runs on the outer side of the eyeball under the lacrimal gland. The muscle is inserted by a thin tendinous expansion on the sclera in front of the equator. The abducens nerve supplies it on its medial surface.

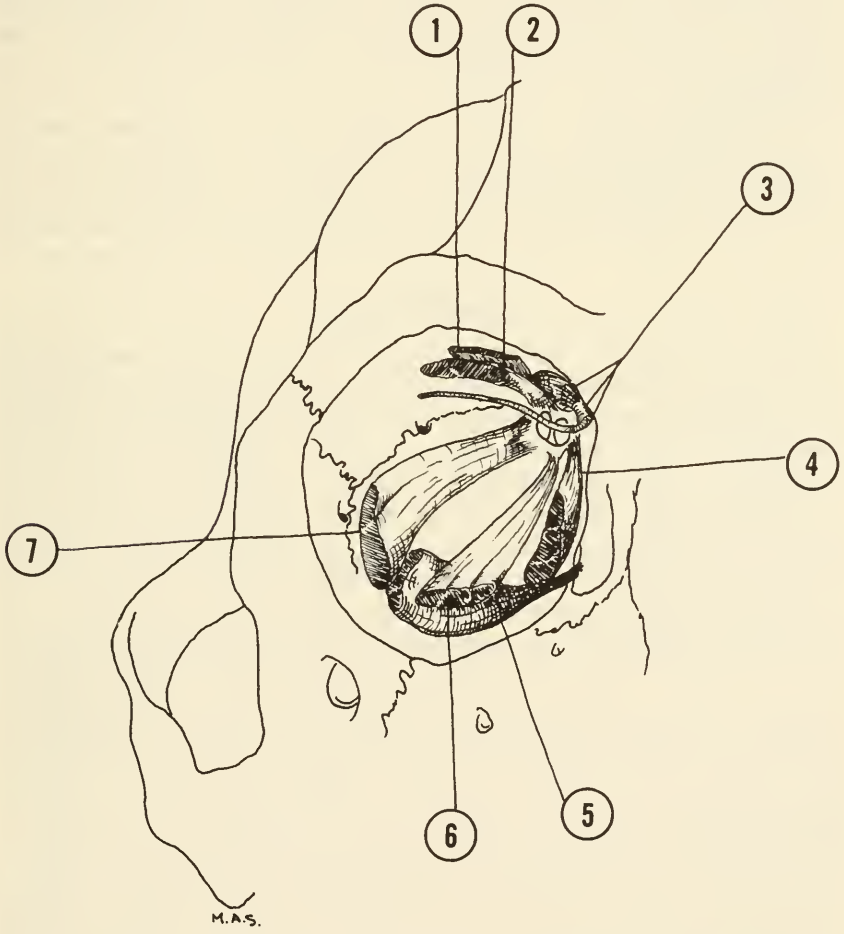

FIGURE 10.—Ocular muscles (1, m. levator palpebrae superioris; 2, m. rectus superior; 3, m. obliquus superior, its pulley and tendon; 4, m. rectus medialis; 5, m. obliquus inferior; 6, m. rectus inferior; 7, m. rectus lateralis).

M. rectus medialis: Arising from the medial border of the optic foramen by means of the tendinous ring, its large transversely flattened belly runs forward below that of m. obliquus superior. The ethmoidal branches of the nasociliary nerve accompanied by the corresponding vessels separate the two muscles. Insertion is by an aponeurotic expansion on the medial side of the sclera rostrally to the equator. The lower division of the oculomotor sends a branch to the lateral aspect of the muscle.

M. rectus inferior: It lies on the floor of the orbit between the periorbita and the eyeball with its fascial sheath. Origin is by the tendinous fibers of the common ring from the lower border of the optic foramen. The long belly passes forward to be inserted on the sclera in front of the equator and in line with the attachment of m. rectus superior. The lower division of the oculomotor nerve innervates this muscle.

M. obliquus inferior: It has a fibrous origin at the lower part of the posterior lacrimal crest from which a narrow and tendinous band is directed medially and gives rise to the fleshy bundles of the muscle. Its expanded belly crosses the insertion of the rectus to end on the sclera. It is supplied by the lower division of the oculomotor nerve.

Lingual Group

There is a torus on the inner surface of the howler's mandible. It is continuous with the linea mylohyoidea and forms the upper margin of a variably developed simian pit (see Scott, 1963). This is subdivided by a short sagittal crest running from the torus to the basis mandibulae which constitutes the lower margin of the depression.

M. genioglossus: This paired muscle arises at each side of the midline from the corresponding subdivision of the simian pit (fig. 5). It is initially formed by mixed fleshy and tendinous fibers arranged into a craniocaudally compressed structure. The muscular fascicles are directed toward the tip, lower surface and root of the tongue (fig. 7). Fibers along the midline intercross with those of the intrinsic lingual muscles and are inserted on the lateral aspect of the medial lingual septum. The lateral bundles of the genioglossus reach the hyoglossal membrane after forming an elongated belly under cover of m. hyoglossus, below the intrinsic lingual musculature and above the geniohyoid and the hyoid bulla. Sirena (1871) describes two portions in this muscle, the genioglossus proper and that which he calls geniohyoideus profundus. The first goes from an origin equal to the one I found, to the tongue and hyoglossal membrane, the deep part attaches to the hyoid bulla.

Nerve supply: N. hypoglossus.

Function: Its contraction pulls the root of the tongue and the

whole organ forward. The muscle must therefore be of importance in the action of sticking the tongue out as in the premating behavior of females (see Carpenter, 1934). It also probably plays a role in opening the thyrohyoid canal (Schön, 1964a).

M. hyoglossus: It is a large and well developed muscle extended from the cornu branchiale I and the hyoid to the sides of the tongue (fig. 3). Its fleshy bundles originate from the whole length of the said cornu, the capsule of the hyoid-cornual articulation and the tentorial and subtentorial surfaces of the bulla. Cornual fibers appear to be continuations of those of m. thyrohyoideus across the surface of the large hyoid horn. Hyoglossal fascicles at first are almost horizontally directed toward the tongue, becoming increasingly less oblique until those of bullar origin ascend rather vertically. On reaching the tongue some cornual fibers pass between the genioglossus and the tentorium to meet a similar group from the opposite side as described elsewhere (Schön, 1964a); the rest intercross with the intrinsic lingual muscles after covering the lateral aspect of the genioglossus. A similar muscle was also found by both Sandifort (1834) and Sirena (1871).

Nerve supply: N. hypoglossus.

Function: Retractor of the tongue.

M. styloglossus: This is a variable structure. It was present in three of my males and I reported this finding earlier (Schön, 1964a), but it was absent in another male and a female subsequently studied. Only a fine tendinous structure not easy to isolate from the stylomandibular ligament and parotid fascia represents the styloglossus in these two specimens. It leaves the proximal end of the stylopharyngeus and running between the two styloid muscles ends on the lateral side of the superior constrictor. Lampert (1926) did not find the styloglossus in his two adult males. Sirena (1871) declares it to be present and so does Sandifort (1834). Typically, the muscle leaves the inner border of the stylohyoideus tendon and proceeds distally to reach the pars lingualis of the superior pharyngeal constrictor.

Nerve supply: N. hypoglossus.

Function: Pulling back the tongue.

No information is given about the intrinsic muscles of the tongue because they could not be well revealed by dissection.

Comparative anatomy of the lingual group.—This group of muscles was studied by Houpert (1927) in *Ateles*, and Lampert (1926), who observed them in the spider, woolly, and ring-tailed monkeys. Their findings in general indicate attachments and relations similar to those of the howler, but an evident lesser development, most manifest in the hyoglossus. Lampert (1926) saw continuation of the thyrohoideus and hyoglossus fibers in *Cebus* but not in *Ateles*. Houpert (1927), on the other hand, does describe such an uninter-

rupted condition between the two muscles of his adult female spider. The muscle is also weakly differentiated in *Brachyteles* (Hill, 1962). The styloglossus is present in *Cebus* (Lampert, 1926), *Ateles* (Bijvoet, 1908; Houpert, 1927; Lampert, 1926), *Lagothrix* (Lampert, 1926) and *Brachyteles* (Hill, 1962). The variability of this structure in *Alouatta* indicates, perhaps, that it has not yet attained a stable pattern in this genus.

Muscles of the Trunk

Expaxial Musculature

The epaxial group of muscles supplied by the dorsal rami of the spinal nerves occupies the regions between the back of the skull and the end of the tail. They are contained in the neck and trunk within the space formed by the nuchal and thoracolumbar fasciae with the vertebrae and part of the ribs. A tough fibrous fascial continuation of the first two into the tail surrounds the caudal muscles, forming sheaths for their many tendons.

The nuchal and thoracolumbar fasciae (figs. 11, 12): An extensive aponeurotic lamina covers the splenius and the erector spinae. It is particularly strong and evident in the low thoracic and lumbar regions. Its fibers arise from (1) the ligamentum nuchae, (2) spines of the lower cervical, all thoracic and lumbar vertebrae, (3) the corresponding interspinal ligaments, and (4) the crista sacralis mediana. These fascicles follow a laterally transverse direction to end (1) on the whole extent of the nuchal crest under cover of the origins of trapezius and rhomboideus, (2) in the cervical region, on the posterior tubercle of all transverse processes, (3) in the thorax, on the body of each rib just lateral to the attachment of m. iliocostalis, and finally, (4) in the loins, the fibers of the fascia turn medially at the lateral border of the erector mass and lining its deep surface reach the tip of all lumbar costal processes. Both the latissimus dorsi and the posterior inferior serratus arise from the thoracolumbar part which also gives rise to the bundles of the internal oblique and transversus abdominis (figs. 11, 12). The lateral attachment of the sacral fascicles of the fascia is on the iliac crest, from the posterosuperior iliac spine dorsally to the craniad projecting spine of the crest ventrally. This last structure is described with the insertions of m. obliquus externus abdominis. Between the median sacral crest and the iliac tuberosity the fascia is thin and fused with the underlying tendinous superficial fibers of the erector spinae and the caudal musculature. In the neck m. splenius is contained within a split of the nuchal fascia which in both the cervical and thoracic regions sends a sagittal septum between the iliocostalis and longissimus muscles.

Superficial Oblique System

It is represented by a single muscle, the splenius.

M. splenius: This strong muscle originates from the ligamentum nuchae, between the spine of the axis and that of thoracic vertebra 1. Some of its fibers are often displaced laterally and arise directly from the nuchal fascia. The flattened and fleshy belly is trapezoid-shaped. Its short parallel side limits, with that of the muscle from the opposite side, a small triangular space over the occipital and suboccipital regions. Insertion takes place on the outer half of the superior nuchal line deep to the endings of m. rhomboideus and trapezius (fig. 5). There was no splenius cervicis.

Sirena (1871) includes the first two or three thoracic vertebrae in the origin of the muscle and, more interesting, describes the fibers along its lateral margin as being tendinous and inserted on the transverse process of the atlas. Hill (1962) also mentions such a vertebral ending.

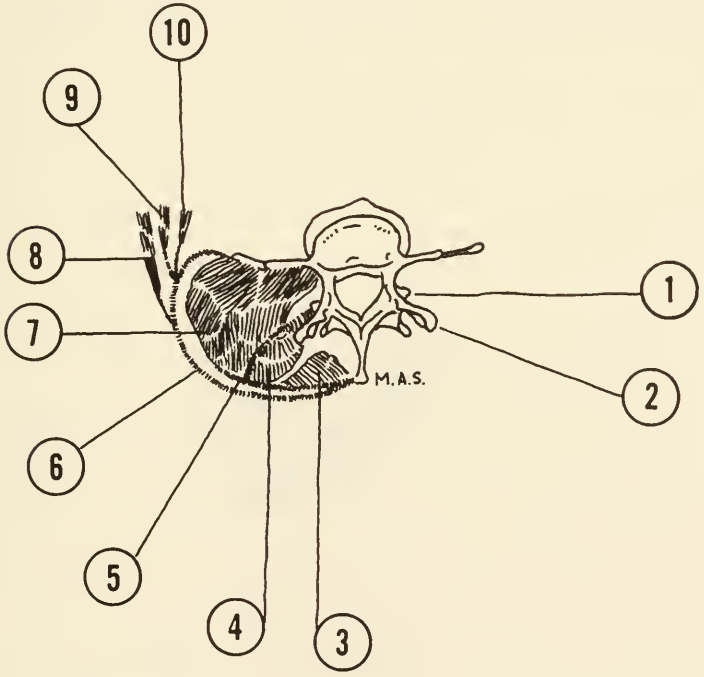

FIGURE 11.—Section at the level of L4 showing arrangement of thoracolumbar fascia (1, anapophysis; 2, metapophysis; 3, m. spinalis; 4, m. longissimus; 5, aponeurosis sacrospinalis and its septum or attached sheet; 6, thoracolumbar fascia; 7, m. iliocostalis; 8, m. obliquus externus abdominis; 9, m. obliquus internus abdominis; 10, m. transversus abdominis).

This fact, which I could not verify, would correspond to the presence of a splenius cervicis in the howling monkey.

Nerve supply: A branch from the dorsal primary ramus of CIII.

Long System

Its muscles form a longitudinal mass which covers the deep oblique system and, more laterally, lies over the rib cage. Two of them, m. iliocostalis and m. longissimus, have a common origin in the lumbar region from a tough, extensive, and tendinous sheet, the aponeurosis sacrospinalis (figs. 11, 12, 13). M. spinalis lies medially to the other two and has a separate origin from the same lamina (figs. 11, 12). The longissimus is continued into the tail by m. extensor caudae lateralis and the two abductors.

The aponeurosis sacrospinalis (figs. 11, 13): Strong tendinous fascicles arise from (1) the spines of most thoracic, all lumbar, sacral, and the first two caudal vertebrae, and (2) the corresponding ligamenta supraspinalla. They all run craniolaterally and are joined by similar fibers arising from (3) the dorsal half of the iliac crest and the region of the posterosuperior iliac spine. In this manner a shiny lamina is formed over the long muscles of the back. It extends laterally a little

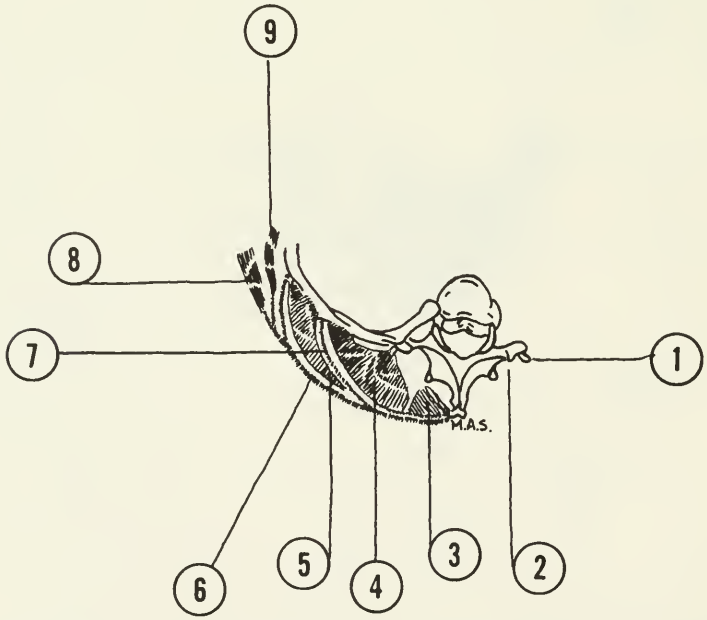

FIGURE 12.—Section at the level of T9 showing arrangement of thoracolumbar fascia (1, anapophysis; 2, metapophysis; 3, m. spinalis; 4, m. longissimus; 5, m. iliocostalis; 6, thoracolumbar fascia; 7, sagittal septum; 8, m. latissimus dorsi; 9, m. serratus posterior inferior).

beyond a plane passing through the tip of the costal processes in the loins and just short of the costotransverse articulations in the thorax. In the former region a sagittal septum given off from its deep aspect is inserted on a poorly marked line which joins the anapophysis and metapophysis in each vertebra (fig. 11). This partition I call the attached sheet of the aponeurosis which is thereby divided into a medial and a lateral half. Kohlbrugge (1897) describes a similar structure in *Semnopithecus* (=*Presbytis*) and the pongids, emphazising the distinctness of this aponeurotic lamina from the fascia lumbodorsalis (thoracolumbar fascia). Howell and Straus (1933) did not establish this difference between the thoracolumbar fascia and the aponeurosis sacrospinalis in the rhesus monkey. According to them, both m. longissimus and m. spinalis arise from the deep surface of the lumbodorsal aponeurosis.

M. iliocostalis (figs. 11, 12, 13): The more lateral part of the long system has two portions: (1) M. iliocostalis lumbothoracis. Origin is by fleshy fibers from (a) the iliac crest and the cranially projecting spine, and (b) the lateral surface of the attached sheet and under surface of the sacrospinal aponeurosis on its lateral half (fig. 11). Additional fibers are contributed to the deep surface of the muscle in the form of fleshy digitations arising from most if not all ribs. The lumbar insertion is by fleshy bands attached to the costal processes and the last two or three ribs. In the thorax, m. ilicostalis forms several tendons at its lateral border and these end on a small spine found at the angle of approximately the first nine ribs. The distance between the angle and the tubercle is increasingly reduced toward the neck until these two points are very close in the first rib. The highest tendon reaches the posterior tubercle of C 7. (2) M. iliocostalis cervicis lies medially to the cranial part of the lumbothoracis and arises by fleshy slips from the first three ribs. The short fusiform belly inserts by two tendons on the posterior tubercle of the fifth and sixth cervical vertebrae.

M. longissimus (figs. 11, 12, 13, 14): It lies medial to the iliocostalis from which it is separated in the thorax and neck by the sagittal septum of the nuchal and thoracolumbar fasciae, and in the loin by the attached sheet of the sacrospinal aponeurosis. The muscle is composed of two parts: (1) M. longissimus lumbothoracis arises in the lumbar region from the sacrospinal aponeurosis both on the under surface of its medial half and medial aspect of the attached septum. In the thorax its superficial fleshy fibers are a continuation of the aponeurosis sacrospinalis. The muscle receives additional contributions from the metapophyses of the first two lumbar and last two or three thoracic vertebrae. Up in the high thoracic region it occasionally has muscular fascicles coming from the metapophyseal tubercles of T 1 to T 3. The

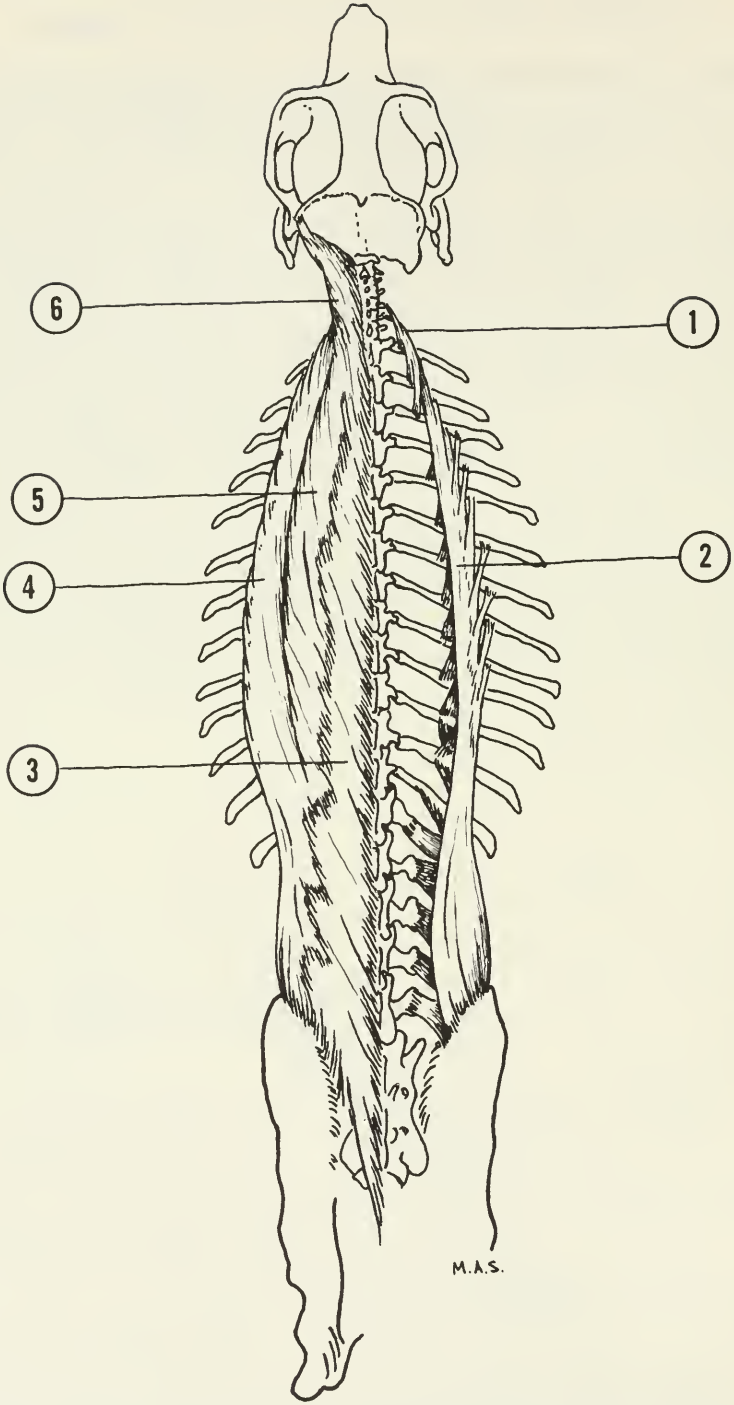

FIGURE 13.—The long system of epaxial muscles (1, m. iliocostalis cervicis; 2, m. iliocostalis lumbothoracis; 3, aponeurosis sacrospinalis; 4, m. iliocostalis; 5, m. longissimus lumbothracis; 6, m. longissimus cervicis et capitis).

long mass formed from these different sources reaches the neck as a cervical extension and gives off digitations from its deep surface to the underlying bony structures. Mediocranially oriented fibers separate toward the anapophyses of all lumbar and thoracic vertebrae (only anapophyseal tubercles are involved in the first thoracic segments). The cervical extension sends slips of the same direction to the posterior tubercle of all cervical vertebrae, although C 1 is usually excluded. These insertions are entirely fleshy on the lumbar and lower thoracic regions, increasingly tendinous in the thorax and again muscular in the neck. Fibers with laterocranial direction leave the deep surface of the muscle and run toward the lower border of all ribs where they are inserted between the tubercle and the midpoint between the tubercle and the angle. These digitations are flat and broad, fleshy caudally up to about the ninth rib, but increasingly tendinous in the thorax. The last one or two ribs may not receive any. (2) M. longissimus cervicis et capitis. These two commonly distinct muscles are more or less fused into a single mass in *Alouatta*. It lies medial to the cervical extension of the lumbothoracal part and arises by fleshy fibers from (a) the crest formed by the articular processes of the last five or six cervical vertebrae, and (b) the first three or four metapophyseal tubercles where they are partially fused with the attachments of the cervical extension. Insertion takes place after a craniolateral path into the posterior tubercles of the last six cervical vertebrae and by a large round tendon on the postmastoid crest (fig. 5).

M. spinalis (figs. 11, 12): It is the more medial component of the long system lying between m. longissimus and the spines of all cervical, thoracic, and lumbar vertebrae. It is divided into two parts. (1) M. spinalis lumbocervicalis is covered by the sacrospinal aponeurosis and itself lies over the deep oblique musculature. The long mass has a segmented arrangement and extends from about S 2 up to the neck. In the sacral and lumbar regions fleshy fibers arise from the under surface of the sacrospinal aponeurosis medially to the origins of longissimus and are inserted on the spinous processes. Those close to the midline are quite short, whereas the more lateral fascicles extend for a longer distance and form a deep tendon which ends on a spine about five vertebrae cranial to its origin. This attachment lies in close relation to that of the corresponding segment of the deep oblique system. In the upper thoracic and cervical regions the fibers of m. spinalis arise from the sacrospinal aponeurosis and those closer to the midline from the corresponding vertebral spines. The segments are now shorter, bridging only three vertebrae, and do not have tendinous endings. Highest insertion is on the spine of C 4 or 5. (2) M. spinalis capitis is formed by fascicles arising from the aponeurosis and the spinous processes of C 6 to T 4. They constitute a voluminous muscle

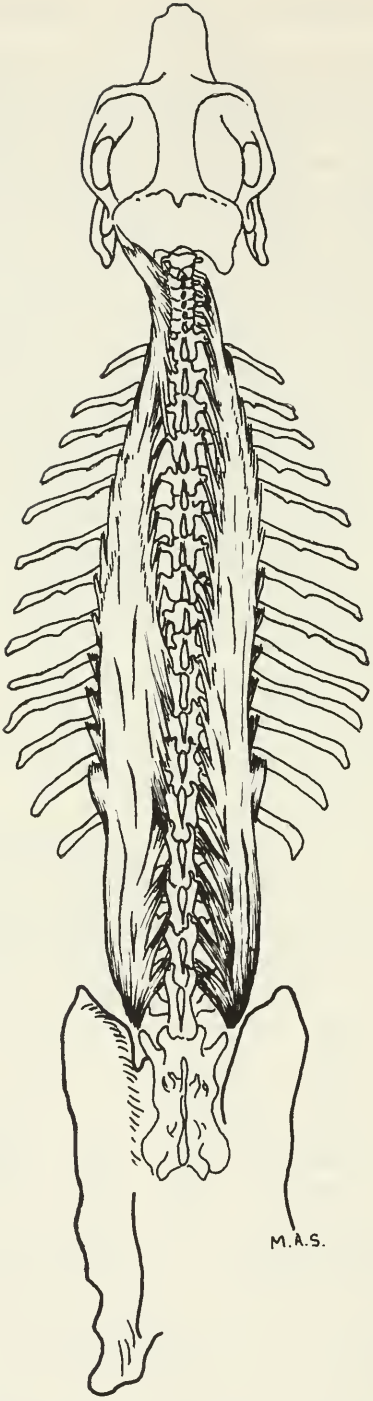

FIGURE 14.—M. longissimus: Right side, shows the cervical extension, the costal, transverse cervical, and anapophyseal insertions; left side, shows in addition the metapophyseal origins and m. longissimus cervicis et capitis.

fused with the laterally lying m. semispinalis capitis with which it is inserted on the occipital squama between the splenius and the suboccipital muscles (fig. 15).

M. extensor caudae lateralis: This is a long and strong muscle extending from the lumbar region all the way to the end of the tail. Its proximal fleshy belly changes distally into several tendons. In the loins the muscle lies against the pedicles of the lumbar vertebrae, over their costal processes, and is separated laterally by a very well-defined space from the origins of longissimus on both sheets of the sacrospinal aponeurosis. It then occupies the lateral sacral grooves, where it is found between the abductors and the medial extensor of the tail. Caudally, the subdivided belly and its tendons run along a trough formed in the proximal vertebrae by the pedicles, the articular and the costal processes; in the distal ones by the cranial articular processes, the body and the very much modified costal and distal articular processes. Origin is from (1) the anapophyses of the last four or five lumbars, (2) the tubercles of the intermediate sacral crest, and (3) the proximal articular processes of all caudal vertebrae. Insertion takes place by 24 or 35 tendons individually attached to the proximal articular processes of each of the caudal vertebrae, superficial to the distal segments of the muscle. The first ends variably from Cd 3 to Cd 5. The caudal aponeurosis provides individual fibrous covers for the subdivisions of the belly and their respective tendons.

M. abductor caudae medialis: This muscle is found only in the sacral and proximocaudal regions, between and almost completely covered by both the extensor and the abductor caudae lateralis. Its fleshy fascicles originate from (1) the iliac tuberosity and the posterosuperior iliac spine, and (2) the dorsal sacroiliac ligaments. Insertion is on the costal processes of the first four caudal vertebrae by an equal number of tendons fastened to the cranial border of these structures. This attachment is marked by a spine.

M. abductor caudae lateralis: It has a segmented arrangement and is larger than the medialis. Origin is from (1) the sciatic margin above the greater sciatic notch and (2) the costal processes of caudal vertebrae. A unit spans four segments proximally but is shorter toward the end of the tail. Insertion is also on the costal processes.

Sirena (1871) is the only one who has previously dealt to some extent with the long muscles of the back in *Alouatta*, but his description of the different parts of the system is incomplete. This is probably due to the great difficulties which one finds in following the details of the several tendinous and fleshy attachments. He refers to the iliocostalis as m. sacro-lumbalis and adds that it lacks a m. cervicalis ascendens. Nishi (1919) has explained that what Arnold called m. cervicalis ascendens in man is just the iliocostalis cervicis of other

authors. I think Sirena (1871) used the name in Arnold's sense and not in that of trying to indicate a homology between a muscle of the howler and the m. cervicalis ascendens of marsupials as described by Coues in 1872. For these reasons it can be assumed that none of the

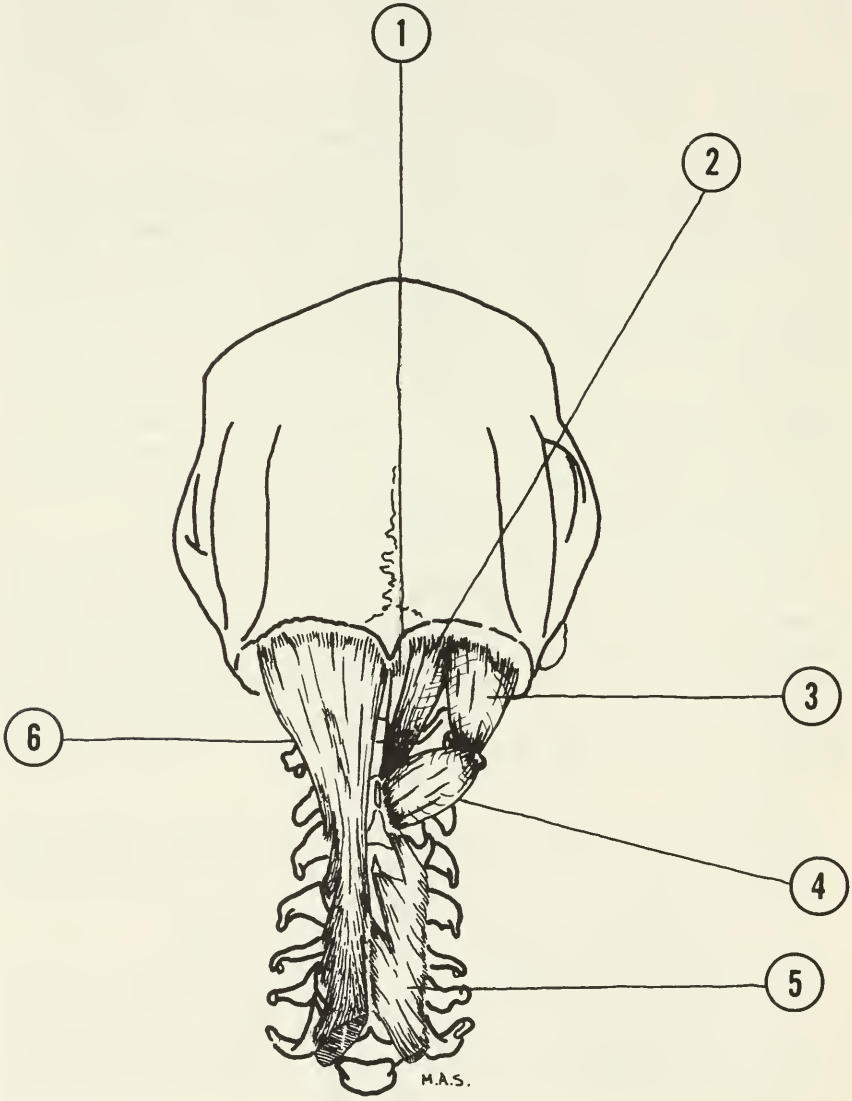

FIGURE 15.—Deep oblique and short system muscles in the neck (1, m. rectus capitis posterior minor; 2, m. rectus capitis posterior major; 3, m. obliquus capitis superior; 4, m. obliquus capitis inferior; 5, m. multifidus; 6, mm. semispinalis et spinalis capitis).

three specimens of *Mycetes fuscus* (=*Alouatta fusca*) studied by Sirena (1871) had an iliocostalis cervicis. The sacrolumbalis reached only the transverse processes of C 7.

According to Sirena (1871), a m. longissimus dorsi (m. longissimus lumbothoracis) has an origin from the dorsal surface of the sacrum and one insertion, by means of aponeurotic fibers, on the spinous processes of the last nine thoracic vertebrae. The description agrees in other details with mine. The sacral origin I regard as doubtful, and probably is an error. The lateral sacral canal is occupied by m. extensor caudae lateralis which is clearly separated from the longissimus, and the medial canal is taken by the extensor caudae medialis. The aponeurotic ending on the thoracic vertebrae is more likely a misinterpretation of the sacrospinalis aponeurosis in that region. Sirena (1871) describes a m. transversalis cervicis (m. longissimus cervicis) and m. complexus minor (m. longissimus capitis) separately but adds that these two muscles are fused. The origin of the first is assigned to the transverse processes of the first two or three thoracic vertebrae and C 7. Sirena (1871) does not cover m. spinalis at all. In the tail of *Alouatta fusca* a m. sacrococcygeus superior corresponds to the extensor caudae lateralis and an m. ileococcygeus superior to the two abductors.

Nerve supply of the long system.—The muscles of the long system are all supplied by the dorsal rami of the corresponding spinal nerves; in the cervical and upper thoracic regions by the lateral branches of these rami, in the lower thoracic and lumbar by their medial branches, and in the tail by the dorsal branches of the corresponding sacral and caudal nerves.

Deep Oblique System

The muscles of this group are not well differentiated except for m. semispinalis capitis, the rotatores, and the extensor caudae medialis. The total mass appears to be small in relation to that of the long system, and all its fibers are craniomedially directed from metapophyses to spinal processes.

M. semispinalis lumbocervicalis et multifidus: This is a compact and segmentally arranged column present along the vertebral grooves of the upper lumbar, thoracic, and cervical regions. Its caudal limit has been arbitrarily assigned to the metapophysis of either L3 or 4, as the whole transversospinal system is continuous with the medial caudal extensor without apparent interruption. The fibers of one segment arise from a metapophysis and proceed cranially to insert on the tip and caudal border of a spinous process five (thoracocervical portion) or six (lumbothoracal portion) segments removed from their origin. The deeper fibers of each unit bridge only three or four vertebrae and

have their highest insertion on the enlarged and bifid spinous process of the axis (fig. 15). The longer and more superficial bundles reach cranially only to the spine of C 4. The segments of the midthoracic region are thinner than the rest.

M. semispinalis capitis (fig. 15): This powerful and well-developed muscle has a fleshy origin from the articular processes of the last five cervical vertebrae, and by short tendinous fascicles from the metapophyseal tubercles of T 1 to T 4. All these bundles are fused with m. spinalis capitis into a single thick belly attached to the occipital squama. Spinalis fibers are medial to those of the semispinalis of which those coming from the metapophyseal structures present a short tendinous interruption in their middle (biventer cervicis).

Mm. rotatores: They constitute the deepest stratum of the oblique system and are present only in the thoracic region. The rotatores are segmentally arranged into pairs. A rotator brevis goes from a metapophysis to the spine of the vertebra just craniad and a rotator longus passes up to the spine of the second vertebra in the same direction.

M. extensor caudae medialis: This muscle is the caudal extension of the deep oblique system and occupies the vertebral groove of the lower lumbar vertebrae, and its extension into the sacral and caudal regions. The extensor medialis is segmented throughout its extent. A typical unit, such as is found in the proximocaudal region, is composed of fleshy fibers with origin in the spinous tubercles of two adjacent vertebrae and the ligaments joining them. They run caudolaterally, forming a tapering belly which is continued by a round tendon. This attaches to the proximal articular process of the vertebra four segments caudally removed from the first included in the unit.

According to Sirena (1871), M. complexus maior (m. semispinalis capitis) arises from (1) the transverse processes of the last six cervical and first five thoracic vertebrae, and (2) the spines of T 1 to 4. Bundles with a spinous origin correspond, in my opinion, to m. spinalis capitis, which is fused to the capitis part of the deep oblique system. His observation of an origin from the transverse processes of the cervical vertebrae is not correct. M. longissimus cervicis et capitis occupies the space between the transverse and the articular processes in that region (see fig. 14). It lies lateral to the elements of the deep oblique system which, therefore, cannot arise from the said transverse processes, but from the crest formed by the articular ones of the cervical vertebrae (see fig. 15). Sirena (1871) describes the complex of the semispinalis and multifidus as extending from the spine of the axis to the sacral region where it is said to continue into the tail as the m. lumbosacrococcygeus of Vicq d'Azyr (m. extensor caudae medialis). He does not differentiate between rotatores breve and longi.

NERVE SUPPLY OF THE OBLIQUE SYSTEM.—Dorsal branches of the corresponding segmental nerves innervate the muscles of this system.

Short System

M. obliquus capitis superior: Origin is by a mixture of fleshy and tendinous fibers, the last being more superficial than the former, from the lateral third of the occiput just medial to the postmastoid crest and below the insertion of m. semispinalis and spinalis capitis (fig. 5). The belly narrows down caudally and inserts by short tendinous fascicles on the tip of the atlantal transverse process (fig. 15).

M. obliquus capitis inferior (fig. 15). This is a stouter muscle with a broad fleshy origin from the lamina and lateral surface of the strikingly developed spinous process of C 2. It passes laterally toward the tip of the transverse process of the atlas, where it is inserted.

M. rectus capitis posterior major: A flat triangular muscle arising fleshily from the intermediate third of the occipital squama, between the insertion of the combined semispinalis and spinalis capitis above, and the large retrocondylar fossa below (fig. 5). The muscle tapers toward its insertion on the cranial margin of the axial spinous process (fig. 15). There is a triangular space between the medial borders of the major recti of each side through which the medial halves of the underlying minor recti can be seen.

M. rectus capitis posterior minor: With a shape similar to that of the major, it is shorter, less strong and arises from the medial third of the occiput, between the attachment of m. spinalis capitis above and the rim of the foramen magnum below (fig. 5). Its fibers run distad partially covered by the major to insert close to the midline on the cranial border of the posterior arch of the atlas (fig. 15).

Mm. intertransversarii laterales et mediales: In the neck fleshy fibers arise from the caudal surface of a transverse process and descend toward that of the vertebra next below. Most of the time they do not show the typical paired condition, only the posterior member being present and inserted in the posterior tubercle. There invariably are strong anterior and posterior muscles between C 1 and 2. The spinal nerve runs in front of, or between the two muscles in the few cases when the pair is complete. In the thoracic region they are increasingly less developed and can be found only up to about the interval T 7 to T 8. A typical lumbar intertransverse arises at a metapophysis. Its bundles reach the anapophysis of the next craniad vertebra and the medially adjacent capsule of the interarticular joint. There are fleshy columns joining the articular processes of the proximal caudal vertebrae and also the tubercles of the intermediate sacral crest.

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Mm. interspinales: In the lumbar region a mixture of tendinous and muscular fibers join the adjacent spinous processes. In the neck, in relation with the underdevelopment of the spines of C 3, 4, 5 and the enlargement of that of the axis, the interspinal muscles are accordingly modified. A pair of well-developed bellies, one at each side of the midline, arises from the lateral surface of the spines of C 5 and 6. They pass upward to end on the flanges resulting from the bifurcation of the axial spinous process.

The four muscles involved in the formation of the suboccipital triangle are regarded by Sirena (1871) as better developed, with relation to the region, than their equivalents in man. He describes paired musculi intertransversarii in the cervical and lumbar regions only. The interspinales of the neck are said to be like those of man and, in the thoracic and lumbar regions, represented by tendinous fibers.

Nerve supply of the short system.—The dorsal ramus of C I passes through the postatlantal foramen and sends branches to all four suboccipital muscles. The obliquus capitis inferior receives also a branch from the dorsal ramus of C II. The intertransversarii and the interspinales are supplied by branches of the corresponding dorsal rami of the spinal nerves.

Function of the epaxial muscles.—They are essentially extensors of the head, neck, trunk, and tail when they contract bilaterally. This role in the first two regions is particularly significant due to the problems introduced here by the weight of the hyolaryngeal structures. This large mass exerts a flexing influence upon the combined craniocervical portion of the animal. Based on the electromyographic studies of the back muscles in man (Morris, Benner, and Lucas, 1962), I think that in *Alouatta* the components of the erector spinae act also as ipsilateral rotators while the members of the deep oblique system are involved in the contralateral action. The complex arrangement of the fascicles of the long and deep oblique systems in the low thoracic and lumbar regions of *Alouatta* suggests that the rotatory role of all these muscles is not fully differentiated.

The caudal extensions of the long and deep oblique systems have attained a considerable degree of differentiation in accordance with the prehensile abilities of the tail. This appendix is used for a wide variety of purposes, from that of securing a hold on the branches while moving, resting, or eating, to others such as manipulating the genitalia (Carpenter, 1934).

With respect to the long system, the origin of longissimus from the metapophyses of the first lumbar and last two or three thoracic vertebrae may perhaps be related to the locomotor habits of the animal. The howling monkey is generally regarded as a sluggish creature, acting more like an arboreal quadruped than as a brachiator. Erikson

(1963) has already pointed out that if we define the spinal regions on the basis of the type of articulations, the number of lumbar vertebrae in *Alouatta* is on the average eight with a range of seven to nine in 21 adult specimens. The opposition to lateral rotation found in the traditionally defined lumbar column is thereby extended cranially to include the low rib-bearing segments of the spine. In apparent agreement with these osteological details is the presence of conspicuous bundles of longissimus arising from the first three or four lumbar vertebrae (in Erikson's sense). Such fascicles would in all likelihood contribute favorably to dorsiflexion movements, but restrict those of lateral rotation. Unfortunately, there is no available information about *Ateles*, *Brachyteles*, *Cebus*, or *Lagothrix* dealing in similar details with the epaxial musculature. Due to this fact my interpretation has to be taken with some reservation until more material either substantiates or negates it.

The presence of a m. semispinalis capitis fused with bundles coming from the spines of C 6 to T 4 which I regard as m. spinalis capitis, could perhaps be another adaptation to the role of extending the head and neck against the flexing influences of the hyolaryngeal organs. De Pina (1930) reports similar spinal fibers from T1 to T5 in the left side of a female *Lagothrix humboldtii* whose right side, however, did not have these origins. Again, absence of comparative information about other cebids demands caution in accepting this interpretation for the fusion of the two muscles.

The situation of a combined longissimus cervicis et capitis, as described by Sirena (1871) and myself in the howler, could also be an adaptation to the problems of balancing the skull and the large voice-producing structures upon the vertebral column. Once more, the lack of related information about other cebids requires caution respecting this opinion.

The remarkable development of the spinous process of the axis is paralleled by the peculiar arrangement of the cervical interspinales. Von Eggeling (1922) noted the proportion of the axial spine which, according to Schultz (1961), corresponds to 214 percent of the mid-sagittal diameter of the body in that vertebra. Such a value is the highest among platyrrhines and is surpassed only by *Pongo* (266%) within the order Primates (Schultz, 1961). These characters are probably another adaptation to the same problem.

Comparative anatomy of the epaxial musculature.—As it has been said in the previous paragraphs, the knowledge about the epaxial muscles in *Ateles*, *Brachyteles*, *Cebus*, and *Lagothrix* is practically zero. With respect to m. splenius, the only differences between the howler and these genera seem to be (1) the number of vertebral segments taken up by its origin, and (2) the variable presence of a

m. splenius cervicis. In *Lagothrix*, the muscle arises from the protuberantia occipitalis externa down to the spine of T 1 or T 2, and in the woolly spider monkey its origin is from the spinous process of the axis to that of T 2 (Hill, 1962). No information seems to be available for *Ateles* in this respect. In *Cebus*, the origin is said to be from the first four ribs (Hill, 1960). Meckel (1828) describes a splenius cervicis in both *S. capucina* (=*Cebus nigrivittatus*) and *S. paniscus* (=*Ateles paniscus*). In the first case the muscle is not separated from the rest of the splenius and is inserted on the atlas. The separation is complete in the spider and its attachment on the first two cervical vertebrae. Hill (1960), nevertheless, asserts that the splenius colli is not differentiated in *Cebus*. His statements may perhaps be interpreted as a generalization for all cebids because it is presented in his account on the myology of these animals and there is no explanation restricting this detail to any of the genera in particular. The suboccipital muscles of the woolly spider monkey as described by Hill (1962) resemble those of *Alouatta*.

Hypoaxial Musculature

The hypoaxial musculature has been arranged by Straus (unpublished) into five groups.

Lateral Group

It includes several muscles of which the scalenes will be the first I shall deal with. The complex scalene mass extends at each side of the cervical spine from the transverse processes of the corresponding vertebrae to the upper ribs. Kohlbrugge (1897) explained that its subdivision in anterior, medius, and posterior as it was proposed in human anatomy by Gegenbaur is not applicable for comparative purposes. Howell and Straus (1933) noted that the three scalene muscles in the macaque form a rather complex group whose components cannot be homologized with those of man. No attempt is made in the case of the howler to imply homologies with the three muscles in man. Their names have been assigned on the basis of their topographical ralations.

M. scalenus brevis anterior (fig. 16): From the anterior tubercle of the transverse processes of C 4 to 6 there arise an equal number of tendinous digitations which soon become fleshy. The lower bundle is stronger and the distal margin of the muscle thicker. The transversely compressed belly descends down and forward in front of the roots of the brachial plexus and the subclavian artery. Insertion is on the pleural border of rib 1, by short tendinous fascicles, at the junction of the anterior with the intermediate third of the costal shaft.

Sirena (1871) says that this muscle is just as in man, but I could not verify a C 3 origin which is usually assigned to it.

Nerve supply: Branches from the ventral rami of C IV to VI.

M. scalenus medius (figs. 16, 17): It is the largest of the three scalenes and separated from the anterior by the brachial plexus and the subclavian artery. Its origin is by fleshy digitations from the anterior tubercle of C 1 to C 6. The muscle broadens in approaching the dorsolateral aspect of the thorax and is anteroposteriorly flattened throughout. It passes superficial to the first two costal digitations of the serratus anterior but under cover of the others (fig. 17). A slip separates off the belly in the neck to be inserted on the anterior tubercle of C 3. The thoracic ending involves a variable number of ribs to which digitations are sent from the deep surface of the muscle. Insertion is on the second, third, and fourth ribs in two males and the

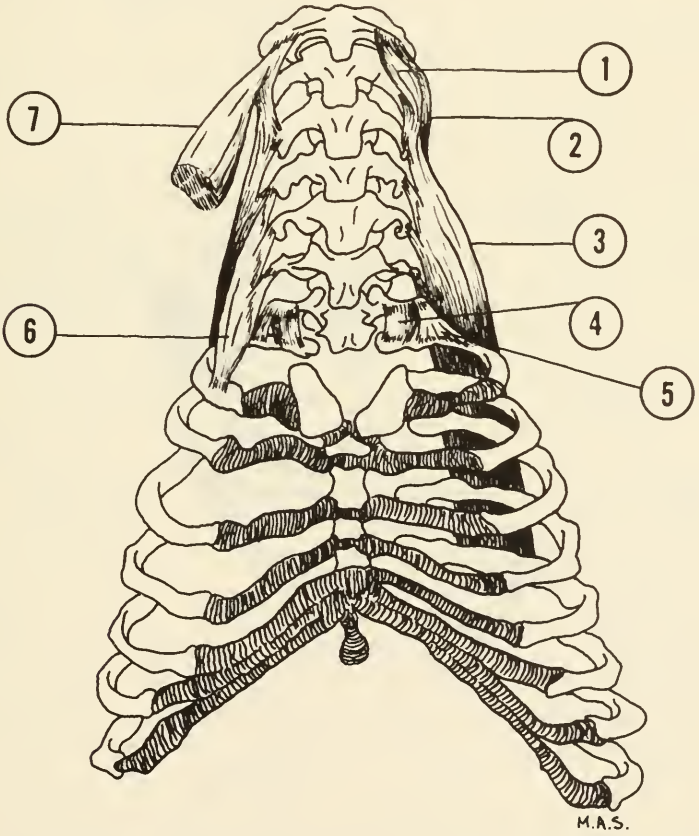

FIGURE 16.—Scalene muscles (1, reinforcing bundle to m. scalenus medius; 2, m. scalenus brevis posterior; 3, m. scalenus medius; 4, m. levator costae primus; 5, m. scalenus medius accesorius; 6, m. scalenus brevis anterior; 7, m. atlantoscapularis anterior.)

female. In the other male it takes place on ribs 2, 3, and 4 on the right side, but 3, 4, and 5 on the left.

Sirena (1871) claims that the costal ending includes all five first ribs and does not describe an origin from C 1. In other respects his information coincides with mine but he refers to the muscle as *m. scalenus posticus*.

Nerve supply: Branches from the anterior rami of C III to VI.

M. scalenus medius accesorius (fig. 16): This triangular muscle is attached by its apex to the tip of the transverse process of C 7. Its strong fleshy fibers radiate out toward the upper surface of the first rib where they are inserted between the sulcus subclavius (this insertion is not marked in the bone) and the angle. The accesorius

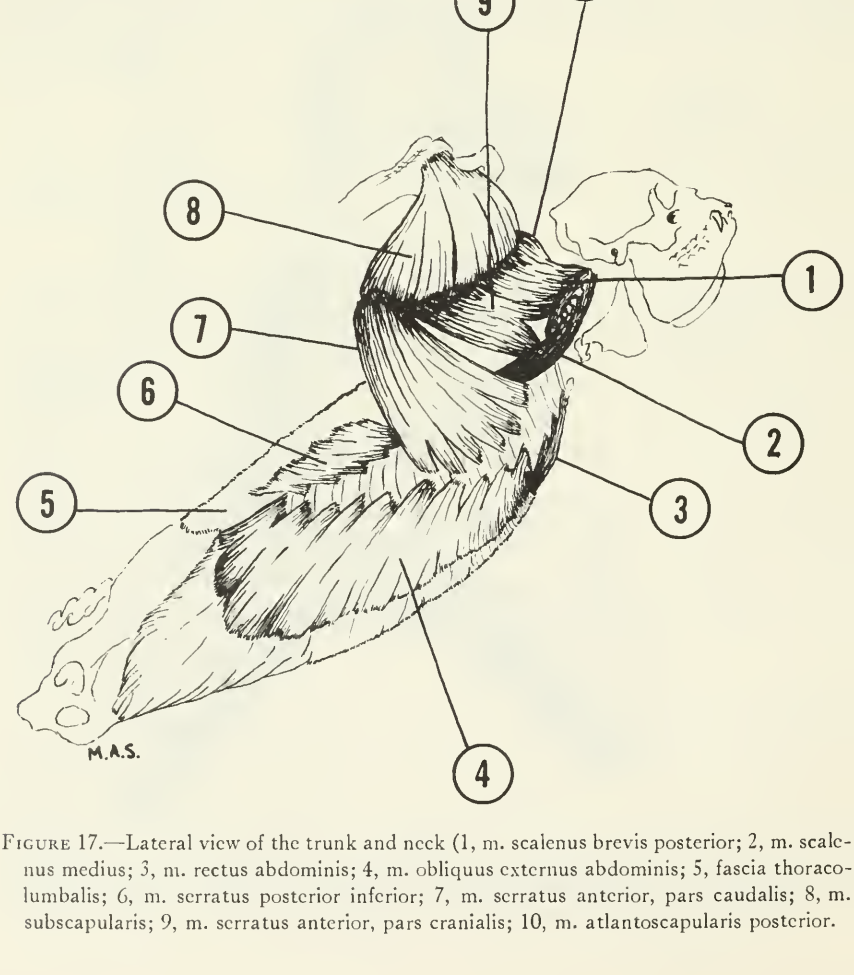

FIGURE 17.—Lateral view of the trunk and neck (1, m. scalenus brevis posterior; 2, m. scalenus medius; 3, m. rectus abdominis; 4, m. obliquus externus abdominis; 5, fascia thoracolumbalis; 6, m. serratus posterior inferior; 7, m. serratus anterior, pars caudalis; 8, m. subscapularis; 9, m. serratus anterior, pars cranialis; 10, m. atlantoscapularis posterior.

lies between the artery and the root of C VIII in front and the deep cervical artery behind. The last vessel separates this scalenus from the levator costae primus. Sirena (1871) indicates the presence of a similar muscle which he names scalenus medius.

Nerve supply: A branch from the anterior ramus of C VIII.

M. scalenus brevis posterior: This muscle is constant but of variable development in different specimens and even in the same individual from one side to the other. It lies dorsolateral to the line of the cervical transverse processes, between the scalenus medius in front and both m. serratus anterior and the atlantoscapularis posterior behind (fig. 17). This scalenus forms a fusiform belly which, arising from the transverse crest of C 1 and the anterior tubercle of C 2 and 3, descends and is firmly anchored by fleshy fascicles to the posterior tubercles of C 4 to 7. In the right side of one male there was an additional attachment to the head of rib 1.

Sirena (1871) does not describe this muscle but the scalenus brevis posterior can be easily missed in cases where its development is reduced. I found one such instance in one male.

Nerve supply: Branches from the anterior rami of C II to V.

Function of the scalene muscles.—The scalenes are known to be elevators of the upper ribs and abductors of the neck. Due to the ventrally convex bending of the cervical spine contraction of the scalenus brevis posterior helps to maintain that curvature and therefore acts as an extensor of the neck, a function which may explain the development attained by these muscles in two of the males.

Comparative anatomy of the scalene muscles.—The complex relations of these muscles and the various terminologies used by the authors to refer to them make their comparative study difficult. It is perhaps for such reasons that not too many students have paid attention to the scalenes. Tschachmachtschjan (1912) studied the scalenus medius in two specimens of *Cebus "flavus"* and one of *Cebus apella*, all males, and one female *Ateles ater* (=*Ateles paniscus*). His description of the muscle is rather sketchy, but enough to allow its identification with what I have called scalenus medius in *Alouatta*. The origin in *Cebus* is said to be from the transverse process of C 2 and the insertion on ribs 3, 4, 5, or on 3 and 4 only. The same muscle in the spider monkey extends from the transverse process of C 2, 3, and 4 to ribs 4 and 5. According to Tschachmachtschjan, the muscle is supplied by the long thoracic nerve in both genera. Forster (1916a) describes the scalenus medius in one *Ateles geoffroy* as lying between the tuberculum anterior of C 2 to 5, reinforced by bundles from C 1, and ribs 1 to 4. The attachment to rib 2 is said by him to be absent on the right side, that to rib 3 on the left. The scalenus anterior of the Forster specimen is just like that in the howler. Furthermore, a

muscle he describes as mm. intertransversarii longi in *Ateles* corresponds, in my opinion, to the scalenus brevis posterior of *Alouatta*. He claims that such a structure is part of the iliocostalis, which in his spider monkey reaches only rib 1 cranially. According to Hill (1962) all three scalenes are present in *Brachyteles*. Their arrangement is comparable to that of the howler and the costal attachment of the scalenus medius is on ribs 2 to 5.

It is interesting to note that the scalenus medius has approximately the same extension over the thorax in all these platyrrhines. Of the four genera for which information is available in this respect, one, *Ateles*, is a very specialized brachiator, and another, *Cebus*, a fairly generalized arboreal quadruped.

Mm. serrati posteriores: The serratus posterior inferior lies over the caudal half of the thorax just lateral to the sacrospinalis and almost entirely covered by m. latissimus dorsi (fig. 17). Its fleshy fibers arise from the thoracolumbar fascia by means of a short aponeurotic sheet which is partially fused to the overlying one of the latissimus (fig. 12). The muscular fascicles run almost transversely laterad forming a variable number of digitations which are inserted on the distal border of the ribs just beyond the angle. Seven such slips attach to ribs 8 to 14 in two 14-rib males; only six are found in the 13-rib male, inserted on ribs 8 to 13. The 13-rib female had eight attached to ribs 6–13. The caudal two or three endings interdigitate with the origins of m. obliquus abdominis externus and are covered by the latissimus dorsi. The serratus posterior superior is represented by transversely directed tendinous fibers more or less fused to the thoracolumbar fascia and running from ribs 2–5 toward the dorsal midline.

Sirena (1871) also found the serratus posterior superior replaced by aponeurotic fibers. They extended across the erector spinae between the spines of C 5 to T 2 and ribs 1 to 4. On the other hand, Ogushi (1920) claims to have seen in one *Mycetes seniculus* (=*Alouatta seniculus*) fleshy fibers attaching to ribs 3 to 4 with aponeurotic fascicles inserted on ribs 2 and 5. The serratus posterior inferior of *Mycetes fuscus* (=*Alouatta fusca*) is said by Sirena (1871) to be even better developed than in man, extending from the spines of the lower six thoracic and first two or three lumbar vertebrae to the last nine ribs, except the fourteenth. According to Ogushi (1920), the costal insertion of the inferior serratus is by fleshy fibers on ribs 8 to 12 and tendinous on the seventh and thirteenth in a 14-rib *Mycetes seniculus* (=*Alouatta seniculus*). Neither of these two authors indicates an attachment to the last rib. It should be repeated that this digitation was found always in both sides of the four animals I studied. It can, nevertheless, be missed because it is almost entirely covered by the slip to the next rib craniad.

Nerve supply: Small twigs from the corresponding intercostal nerves.

Function: The main function of the inferior serratus is accepted to be that of fixing the ribs on which it is inserted. It may also depress these costal segments. By the absence of muscular fibers in the area of the superior serratus the role of elevating the upper ribs in respiration is probably taken over by the scalenes.

Comparative anatomy: The separation between the two posterior serrati appears to be less complete in *Cebus* where the last digitation of the upper and the first of the inferior overlap by ending both on rib 7 (3 individuals) or 6 (one) (Ogushi, 1920). In *Lagothrix* these insertions are on the sixth and seventh ribs with the sixth intercostal space intervening (Ogushi, 1920). In the single howler studied by Ogushi (1920) the two muscles were separated by the sixth rib and its two adjacent intercostal spaces. The two posterior serrati in all of my male specimens were always separated by two ribs and the intervening spaces, the female resembling the woolly monkey. Ogushi (1920) found the widest separation in *Ateles* where the serratus posterior superior inserted on ribs 2 to 4, and the inferior on ribs 10 to 14.

Mm. levatores costarum: Strong triangular muscles are found between the dorsal end of every external intercostal muscle and the corresponding costotransverse ligament. They are all covered by the longissimus system. Every levator arises by its apex from the transverse process of a cranially located vertebra and its fibers fan out caudally to be inserted on the cranial border of the next lower rib just lateral to the tubercle. The tip of every thoracic transverse process presents on a lateral view, (1) a cranially directed tuberosity (metapophyseal tubercle), (2) another directed caudally (anapophyseal tubercle) and (3) a ventrally projecting small eminence for the levator costae. These three landmarks, particularly the first two, become increasingly separated one from the other in lower thoracic levels. The third tends to remain closer to the anapophysis. M. levator costae primus occupies the space between the end of the sixth cervical transverse process and the first rib, where it is inserted from the capitulum to the attachment of the scalenus medius accesorius (fig. 16). The last member of the series ends on the last rib.

Mm. intercostales externi: A typical intercostalis externus extends between the levator costae of the corresponding space dorsally and the proximity of the sternal end of the ribs ventrally. It arises from the lower border of the cranially placed rib and its fibers pass caudally and forward to be inserted on the upper border of the rib below. The muscle is thicker dorsally and is continued between the costal cartilages by the thin membrana intercostalis externa.

Mm. intercostale interni: Their fibers run at right angles to those of the externals. Ventrally, they reach the sternum in the upper six spaces and lower down, the costal cartilages of the seventh to the last rib as these form the caudal margin of the thoracic cage. Dorsally, the internals end at some distance from the costal tubercle, the rest of the intercostal space being filled by the thin membrana intercostalis interna.

M. transversus thoracis: It lies on the deep aspect of the ventral thoracic wall and arises at each side of the midline from the lateral border of the four lower sternal pieces, excluding the xiphoid process. The same number of flat and thin muscular slips is formed, running laterally. The lower of these digitations crosses the seventh and sixth cartilages and takes additional origin on the last before ending on the fifth. The second and third digitations have a similar arrangement with attachments to the fourth and third cartilages, respectively. The fibers of the first have a rather steep craniolateral orientation and are inserted by thin tendinous fascicles on the second costal cartilage.

Mm. subcostales: Only three such muscles are present at each side in the upper part of the thorax. Typically, a subcostal arises on the pleural surface of the body of one rib and its fibers pass caudomedially to be inserted on the body of a rib two costal segments removed. The first connects ribs 1 and 3, the second 2 and 4, and the third 3 and 5.

The pattern of all these muscles in *Mycetes fuscus* (=*Alouatta fusca*) as described by Sirena (1871) is similar to my findings in the *seniculus* species.

Nerve supply: All these thoracic muscles receive branches from the corresponding intercostal nerves.

Function: By their known action upon the ribs all these muscles are accepted as active in the respiratory movements.

M. obliquus externus abdominis (fig. 17): The more superficial of the broad abdominal muscles is a wide and long, partly muscular, and partly aponeurotic sheet extended from the rib cage to the os coxae in a craniocaudal direction and from the thoracolumbar fascia to the linea alba transversely. It arises by a variable number of fleshy digitations from the external surface of ribs 5–13 in a 14-rib male, 4–14 in a 14-rib male, 4–13 in a 13-rib male, and 4–13 in a 13-rib female. This origin follows a concave line open craniodorsally. It begins at about the middle of the fourth or fifth costal body and ends on the tip of the last rib cartilage involved in the origin. The fascicles interdigitate with those of m. serratus anterior (ribs 4–8) and m. latissimus dorsi (ribs 9–12). Some isolated fibers may reach the thoracolumbar fascia between the last rib and the coxal bone. The upper bundles of the muscle have a slight caudoventral slant, the lower ones descend almost

vertically, while the rest follow in an intermediate direction. They all end on the aponeurosis of insertion of the external oblique. This is an extensive membranous lamina whose origin can be followed along a line which, beginning in front of the fourth or fifth chondrocostal junction, passes distally, diverging gradually from the rectus abdominis. At approximately midway between the umbilicus and the pubis it turns rather sharply laterally to reach the dorsal margin of the muscle. The fibers of these aponeurosis have the same orientation as the fleshy elements which they continue. They end on the midabdominal line, the pubis, and the ilium.

The iliac insertion takes place on the outer lip of the acetabular border, from the ventral end of the crest to the origin of the sartorius and tensor fasciae latae. There is at the first point a cranially projecting pyramidal process upon which the broad abdominal muscles are anchored: (1) the external oblique inserts on, and the internal oblique and transversus abdominis arise from its lateral border, (2) the thoracolumbar fascia and the sacrospinalis muscle are attached behind, (3) m. iliacus arises from its anterior surface, and (4) the quadratus lumborum and iliolumbar ligament end medially. I have not found this spine described in previous pertinent works (Hill, 1962; Straus, 1929; Waterman, 1929). In one of my 14-rib males the posterior fleshy fibers of the external oblique reach this process.

The pubic insertion of the external oblique is arranged into medial and lateral crura, and in two of the males a ligamentum reflexum was clearly seen. Fibers of the medial crus attach to the pubic symphysis, pubic crest, and the medial end of the iliopectineal line. Those of the lateral crus end over the laterally remaining part of the linea iliopectinea up to about the iliopubic junction. At this point the line is well marked, presenting sometimes a short, blunt process that may be the homologue of the pubic tubercle. In the male the two crura are separated by a wide and oval superficial inguinal ring, of 2 x 1 cm. approximately. It is smaller in the female. The fibers of the crura meet below the cord, thus completely encircling the ring. The ligamentum reflexum appears as a flat fibrous bundle behind the medial crus.

Between the pubic and iliac endings the caudal free border of the external oblique aponeurosis of insertion bridges over the femoral sheath, and more laterally over the iliac fascia. To both of these membranous laminae the external oblique aponeurosis has some degree of fusion, but does not form an inguinal ligament. I could not demonstrate the presence of a lacunar ligament.

All other fibers of the aponeurosis reach the midventral line of the abdomen where they intercross, forming a linea alba along the apposed medial margins of the two abdominal recti.

The description of this muscle by Sirena (1871) agrees in all details with mine. Nevertheless, his explanation of the contribution of this muscle to the rectus sheath is somehow obscured by wordiness. He indicates that a portion of the muscle corresponds to Gimbernat's ligament (lig. lacunare). In my opinion, the fibers so identified are those which in the specimens I studied make the two crura continuous below the superficial inguinal ring. They are inserted on the pectineal line, but do not show the arrangement which in the human is attributed to this ligament. Hill's account (1962) of the broad abdominal muscles in the howling monkey seems to follow that of Sirena (1871).

Nerve supply: The muscle is innervated by twigs from the corresponding lateral cutaneous branches of the intercostal, subcostal, and iliohypogastric nerves.

M. obliquus internus abdominis: It is also a partly muscular and aponeurotic sheet extended between the ribs and coxal bone in one direction, the linea alba and the thoracolumbar fascia in the other. It arises (1) caudally by short tendinous fibers from the outer half of the free border of the external oblique aponeurosis where this is fused to the fascia iliaca, (2) by fleshy fascicles from the intermediate lip of the acetabular border between the origin of m. sartorius and the pyramidal process, and (3) the origin of the muscle is extended by a fibrous aponeurosis to the side of the thoracolumbar fascia (fig. 11). All muscular elements pass ventrally in a cephalomedial direction, except those from the caudal fifth which arching toward the pubis contribute to form the roof of the inguinal canal. The fleshy fibers end (1) on the distal border of the caudal eight or seven ribs and (2) along a semilunar line at some distance from the rectus abdominis. The aponeurotic lamina here formed contributes to the rectus sheath in various manners. In one male (fig. 18a) it passes entirely behind the rectus abdominis but sends also a weak subdivision in front of that muscle in the lower third of the abdominal wall. In another male (fig. 18b) the aponeurosis divides in the upper three-fourths of the abdomen into two parts, one strong sheet going behind the rectus and the other, a very feeble one, in front. In the lower fourth the whole lamina passes in front. The aponeurosis of insertion of the internal oblique reaches the linea alba behind the rectus abdominis throughout the abdomen in the female and the remaining male (fig. 18c). This extensive lamina is fixed to the last costal cartilage and xiphoid process at one end, to the pubic crest at the other.

M. transversus abdominis: It is weaker than the overlying oblique from which it is not easy to separate. Its caudal origin is by means of short tendinous fibers from the outer half of the free border of the external oblique aponeurosis. Fleshy bundles arise in addition from the inner lip of the entire acetabular border, from the thoracolumbar fascia

(fig. 11), and from the deep surface of the caudal seven or eight costal cartilages. They run transversely to the ventral midline ending on an aponeurosis along a line corresponding roughly to the semilunar of the external oblique in the three males. The female had muscular fibers of very little length which ended shortly after their origin making the aponeurosis a broader layer. This lamina is fused very intimately to that formed by the internal oblique with which it shares its ending. It always passes behind the rectus abdominis, but, in one male (fig.

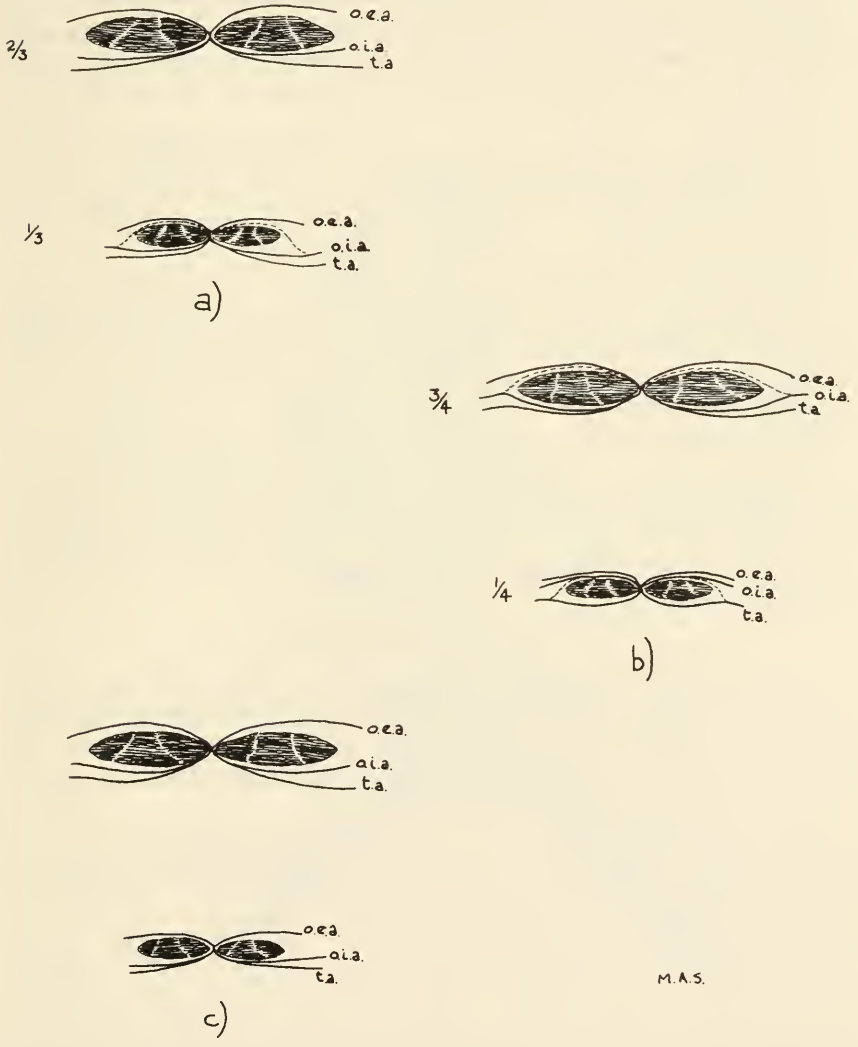

FIGURE 18.—a-c, Cross sections of the formation of the rectus sheath: (o.e.a., m. obliquus externus abdominis; o.i.a., m. obliquus internus abdominis; t.a., m. transversus abdominis).

18b), a fine subdivision is also sent in front of that muscle in the lower fourth of the abdomen.

According to Sirena (1871), the aponeurotic laminae of both the internal oblique and the transversus abdominis behave as in man in the formation of the rectus sheath.

Nerve supply: These last two abdominal muscles are innervated by the lateral cutaneous branches of the thoracoabdominal intercostal, subcostal, and iliohypogastric nerves.

Function: The broad abdominal muscles are important in supporting the viscera while the animal stands or moves on his four extremities. In addition, they are also used in expiration, defecation, parturition, and micturition.

Comparative anatomy: These muscles have in general the same arrangement in all the five genera under consideration. There seems to be, nevertheless, considerable variability among them in the formation of the rectus sheath (see Hill, 1962; Mijsberg, 1915; Miller, 1947; Tschachmachstschjan, 1912; Winckler, 1950).

M. cremaster: The fibers of this muscle form a conspicuous layer over the spermatic cord and the testicles. They arise from the caudal free border of both the internal oblique and the transversus as these muscles form the roof of the inguinal canal. Other fascicles come medially from the pubis.

Nerve supply: The genital branch of the genitofemoral nerve.

M. dartos: It is included in this section for topographical reasons. It is represented by conspicuous and abundant fibers which develop in the membranous layer of the superficial abdominal fascia and accompany its extensions over the penis and testicles. Its nerve supply could not be determined.

Subvertebral Group

M. longus capitis (fig. 19): This is a thick muscular column which, from its origin on the external surface of the basioccipital, descends covered by the prevertebral fascia. Short and tendinous fascicles leave its deep aspect to be inserted on every anterior tubercle and the transverse process of T 1.

M. longus colli: It lies mostly under cover of the longus capitis and has three parts (fig. 19). The superior oblique portion arises by tendinous digitations from the anterior tubercle of C 7 up to C 3. There was always a slip from T 1. These form a flat and fleshy belly which runs craniomedially to insertion on the tubercle of the anterior arch of the atlas. The inferior oblique portion has muscular origins from the intervertebral disks (not the bodies) between T 4 and 1. Insertion is tendinous upon the anterior tubercles of C 7 to C 5. The vertical portion lies between the other two and the midline. It is represented by a series of mostly tendinous bands which arise from

the body of the upper three thoracic and last cervicals and pass cranially along the sides of the anterior longitudinal ligament to be attached on the bodies of the upper five cervical vertebrae.

M. rectus capitis anterior: Its rectangular belly is deep to other subvertebral muscles. Origin is on the basilar process of the occipital immediately in front of the brim of the foramen magnum (fig. 5) and insertion is on the ventral aspect of the lateral masses of the atlas.

M. rectus capitis lateralis: This is a strong and cylindrical muscle with origin from the jugular process of the occipital and adjacent petrous surface (fig. 5). Its fibers reach the lateroventral aspect of the lateral mass where they are inserted on the transverse crest and its extension into the transverse process.

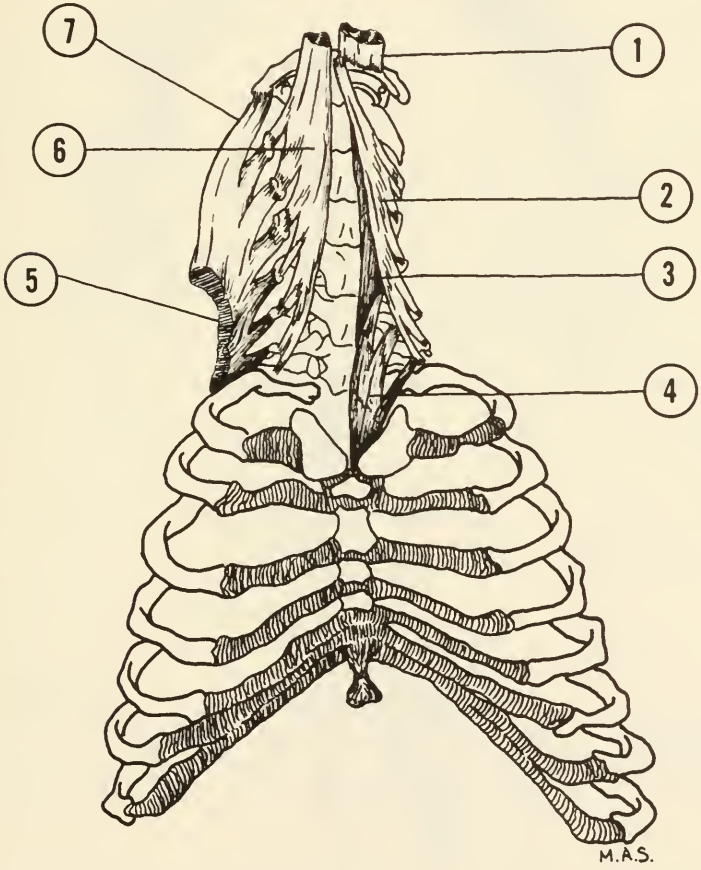

FIGURE 19.—Subvertebral muscles in the neck (1, m. rectus capitis anterior; 2, m. longus colli, pars obliqua superioris; 3, m. longus colli, pars verticalis; 4, m. longus colli, pars obliqua inferioris; 5, m. serratus anterior, pars cranialis; 6, m. longus capitis; 7, m. atlantoscapularis posterior).

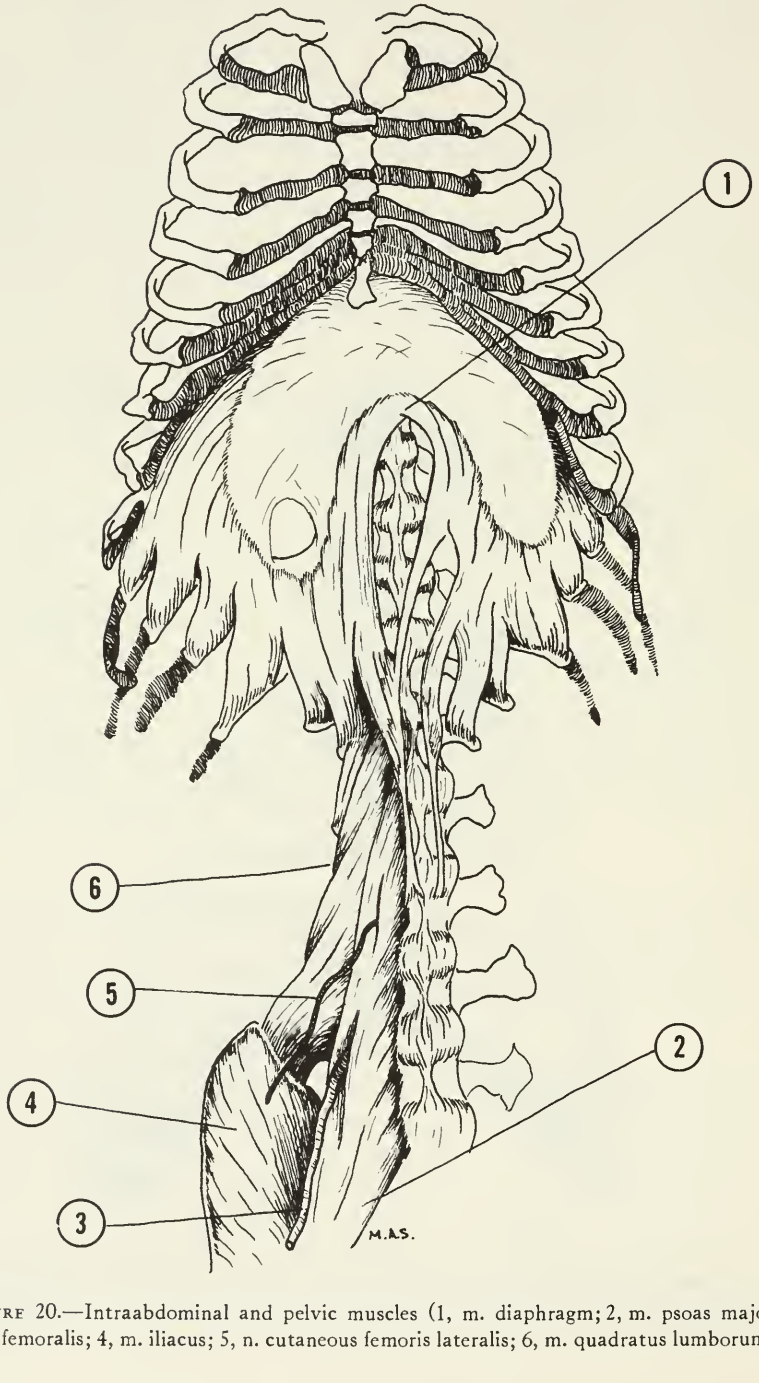

FIGURE 20.—Intraabdominal and pelvic muscles (1, m. diaphragm; 2, m. psoas major; 3, n. femoralis; 4, m. iliacus; 5, n. cutaneous femoris lateralis; 6, m. quadratus lumborum).

Sirena (1871) claims that all of these four paired muscles in the howler are as in man.

Nerve supply of the cervical subvertebral muscles.—They all receive small twigs from the anterior divisions of the cervical nerves. M. rectus capitis anterior and the lateralis are innervated in particular by the anterior division of C I.

Function of the cervical subvertebral muscles.—They flex the head and neck, both ventrally and laterally.

Comparative anatomy of the cervical subvertebral muscles.—Hill (1962) covers both mm. longus capitis and colli in the woolly spider monkey. The first muscle is said by him to arise from the transverse processes of C 5 to 7, the second to be formed by the usual three portions. Forster (1916a) studied these two muscles in *Ateles* where the capitis is assigned an origin from C 3 to 6 and the longus atlantis (pars obliqua superioris musculi longus colli) is said to extend from the costal component of C 3 to the atlas.

M. quadratus lumborum (fig. 20): It is a ventrally compressed muscular column extending along the sides of the lumbar spine from the last thoracic vertebrae to the iliac crest. The muscle is formed initially by fleshy fibers coming from the disk between the two caudal thoracic vertebrae and the body of the last one. The descending belly lies in front of the costal processes from which it receives on its dorsal surface a series of tendomuscular digitations. It is separated from the bodies of lumbar vertebrae 3 to 5 or 6 by m. psoas major. The proximal fibers of the abdominal surface of the muscle end on the tip of the first two costal apophyses, the rest are attached on the iliolumbar ligament and the already described spine of the iliac crest. Insertion also takes place on the last three or four costal processes by fleshy slips from the dorsal surface of the quadratus.

The muscle described by Sirena (1871) in *Mycetes fuscus* (=*Alouatta fusca*) is similar to that of the red howler monkey. He includes also the last two ribs in the origin.

Nerve supply: Branches from the ventral rami of L I, II, and III.

Function: Lateral flexor of the lumbar spine.

Comparative anatomy: The quadratus lumborum of *Brachyteles* is described by Hill (1962) as bilaminar, with origins from the last rib and all costal processes (ventral lamina) or only from that rib (deep lamina). Insertion takes place on the iliac crest at its medial part.

Perineal Group

As in the rhesus macaque (Howell and Straus, 1933), the perineal muscles of *Alouatta* show a clear sexual dimorphism. They will be described separately.

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PERINEAL MUSCULATURE—MALE

M. bulbospongiosus (fig. 21): This muscle surrounds the bulb of the penis and the crura of the corpora cavernosa. Its fibers arise from the longitudinal raphe along the superficial aspect of the bulbus and corpus spongiosum penis. A muscular coat is formed for these structures as the bundles in the anal half of the bulbospongiosus ascend almost perpendicularly toward their insertion in the pars membranacea of the urogenital sphincter, and those in the more ventral portion follow an oblique ventrocranial course around the corpus spongiosum and the crura of the cavernous bodies on their way to

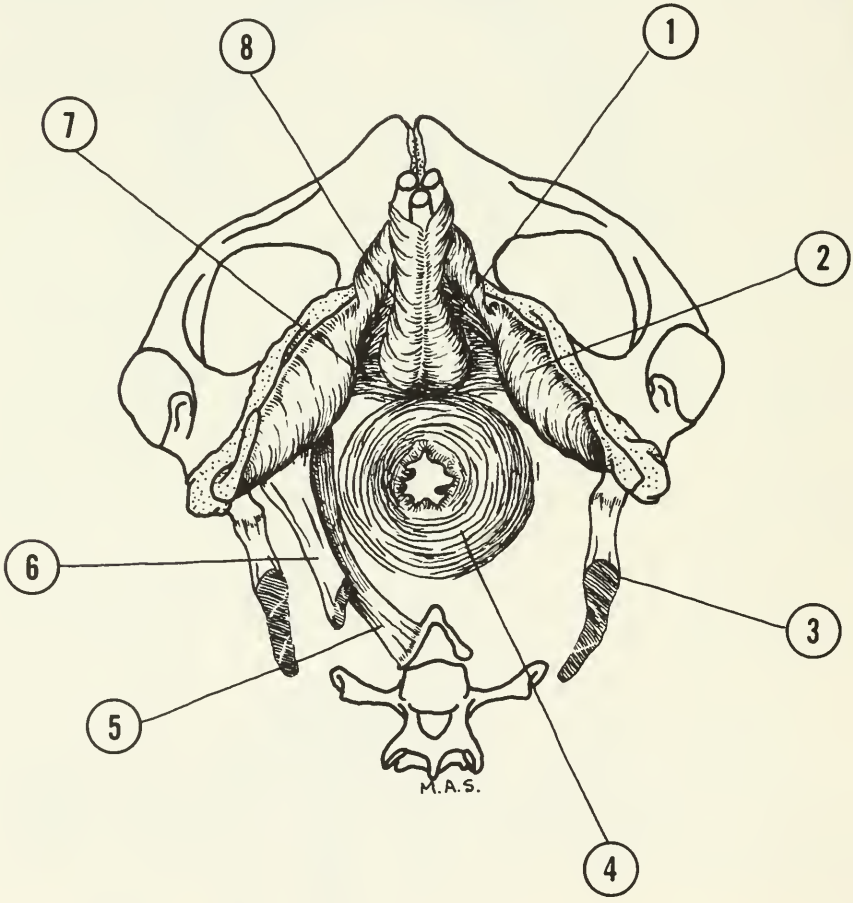

FIGURE 21.—Perineal musculature, caudal aspects of Cd 2 and hemal arch 2 (1, m. ischiourethralis; 2, m. ischiocavernosus; 3, m. ischiocaudalis; 4, m. sphincter ani externus; 5, m. pubocaudalis; 6, m. iliocaudalis; 7, m. sphincter urethrae; 8, m. bulbocavernosus).

the dorsum of the penis. The insertion is on the deep fascia of the penis along the dorsal midline.

M. ischiocavernosus (fig. 21): It is larger than the bulbospongiosus. Origin is from the inner surface of the body of the ischium and the lower pubic ramus from where its fibers pass ventrally covering the corpus cavernosum. They spiral around the crus to reach the dorsum of the penis behind the bundles of the bulbospongiosus. Insertion is on the deep fascia of the penis and the pubic body near the symphysis.

M. ischiourethralis (fig. 21): Some fibers of the former muscle diverge medially to end on the ventral and lateral part of the urethra

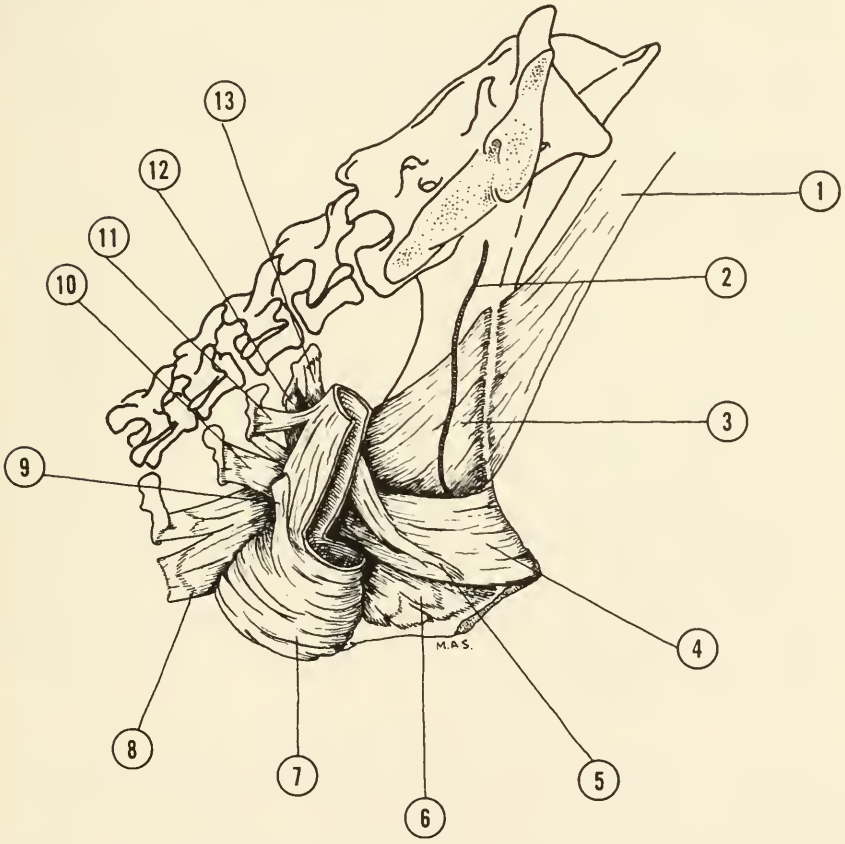

FIGURE 22.—Muscles of the pelvic floor (1, m. psoas minor; 2, n. obturatorius; 3, m. iliocaudalis; 4, m. pubocaudalis; 5, m. retractor recti et urethrae; 6, m. obturatorius internus; 7, m. sphincter ani externus; 8, attachment of m. iliocaudalis to hemal arches 4 and 5; 9, m. caudoanalis of the right side, origin not shown; 10, attachment of m. pubocaudalis to hemal arch 3; 11, m. caudorectalis; 12, m. caudoanalis of the left side arising from hemal arch 1; 13, origin of m. retractor recti et urethrae).

membranacea deep to the bulbus penis and corpus spongiosum penis.

M. sphincter urethrae (fig. 21): It is represented by a rather weak group of muscular fibers which from the midline, deep to the bulbus, pass transversely toward insertion on the ramus inferior of the pubis and the ramus and body of the ischium. Some of its fibers encircle the urethra and the muscle is reinforced in front and laterally of the urogenital canal by m. ischiourethralis. It blends posteriorly with the well developed superficial perineal fascia.

M. retractor recti et urethrae (fig. 22): A long but not so wide band which from the proximoventral part of the tail passes forward around the large rectum and the prostate. It arises from hemal arch I by tendinous fibers which shortly become fleshy. The muscle runs ventrally deep to the pubo- and iliocaudalis, crosses on the lateral aspect of the rectum and prostate between the medial edge of the pubocaudalis and the lateral and anterior puboprostatic ligaments. It ends by fibrous strands on the lateral part of the rectum and prostate up to the anterior border of this gland.

M. caudoanalis: This is a paired muscle which from the tip of the first hemal arch runs ventrocaudally at each side of the midline to join the circular fibers of the sphincter ani externus (fig. 22).

M. caudorectalis: An unpaired muscular band which from the second hemal arch ascends ventrally into the ischiorectal fossa to join the longitudinal fibers of the rectum (fig. 22). It occupies the space left inbetween the two retractors of the rectum and urethra.

M. sphincter ani externus (figs. 21, 22): The circular fibers of this prominent and unpaired muscle form a thick ring around the anal canal. They occupy most of the anal triangle but are separated from the tail by a space filled with fatty clumps. The muscle as a whole and, therefore, the anal canal also have a rather forward position in relation to the caudal appendage. The origin of its fascicles is difficult to identify. They appear to come from an area between the rectum and the urogenital canal where connective tissue is abundant. Some of the anal fibers seem to extend to the rear end of m. sphincter urethrae and m. bulbocavernosus.

PERINEAL MUSCULATURE—FEMALE

M. sphincter cloacae: This is a muscular sheet formed by fibers surrounding the anal and urogenital openings. The fleshy fascicles are supplemented by membranous ones. Some of them encircle only the rectum and correspond to the sphincter ani externus.

M. ischiocavernosus: Less developed than in the male, its fibers end on the fibrotendinous assemblage in the ventral end of the cloacal sphincter above the crura.

M. sphincter urethrae: It is like that of the male, but I did not see an m. retractor cloacae. Both m. caudoanalis and m. caudorectalis are more feeble than in the male specimens.

Sirena (1871) found also the bulbocavernosus of the male to be smaller than m. ischiocavernosus. He describes a m. transversus perinei but the arrangement of fibers in the urogenital diaphragm does not justify, in my opinion, the separate description of a transversus. The retractor recti et urethrae he calls m. levator ani. In other respects the perineal musculature of the animals studied by Sirena (1871) corresponds with that of the red howler. He did not find a m. ischiourethralis, however, and was not able to study the region in a female.

Nerve supply: Mm. bulbospongiosus, ischiocavernosus, and ischiourethralis receive separate twigs from the perineal branch of the pudendal nerve. The sphincter urethrae is innervated by the dorsal nerve of the penis. Several rami from the inferior hypogastric plexus enter the retractor recti et urethrae. I could not determine the nerve supply of either the caudoanalis or caudorectalis. M. sphincter ani externus has the usual innervation by the inferior rectal nerves. The nerve supply in the female is equivalent.

Comparative anatomy of the perineal group.—The perineal musculature was the object of two extensive studies by von Eggeling (1896) and Elftman (1932). The former observed several cebids: 1 female *Ateles ater* (=*A. paniscus*), 1 female *Ateles sp.*, 1 male *Ateles ater* (=*Ateles paniscus*), 2 *Ateles geoffroyi* (=*Ateles geoffroy*), 1 male *Cebus hypoleucus* (=*Cebus capucinus*), 1 male *Cebus fatuellus* (=*Cebus apella*). Elftman (1932) studied only *Cebus* among the platyrrhines. Forster (1926) was concerned solely with the means of fixation of the sphincter ani externus as an indication of adaptation to the mobility of the prehensile tail. Hill (1962) describes briefly the bulbo- and ischiocavernosus muscles in the woolly spider monkey. Nothing seems to have been done about *Lagothrix*. The arrangement of the perineal musculature in *Ateles, Cebus,* and *Brachyteles* appears to be the same (see von Eggeling, 1896; Elftman, 1932; Hill, 1962) as in *Alouatta*. The spider and the howling monkey share the separation of the anal sphincter from the tail by a large space filled with an areolar fatty mass and this muscle is, on the other hand, intimately connected to the urogenital sphincter. Forster (1926) spoke of this condition as an adaptation to the prehensibility of the tail. The poor differentiation of the sphincter urethrae which is formed by a mixture of aponeurotic and muscular fibers, the lack of a fascia diaphragmatica urogenitalis inferior and the absence of an m. levator penis are characters common to all these cebids.

Caudal Group

M. pubocaudalis (figs. 21, 22): This part of the pelvic sphincter is represented by a rather weak muscular lamina whose fibers arise from the back of the pubic symphysis and upper pubic ramus on the iliopectineal line. This origin extends up to about the iliopubic junction. The symphyseal fibers pass backward along the sides of the prostate and rectum with the retractor recti et urethrae intervening. They are joined by the pubic fibers, the most posterior of which have an almost transverse direction. Past the rectum the pubocaudalis is inserted on the second and third hemal arches.

M. iliocaudalis (figs. 21, 22): It is better developed than the pubocaudalis. Its fleshy fibers arise from the linea arcuata below the attachment of m. psoas minor. They pass caudomedially as a muscular sheet superficial to the pubocaudalis, retractor recti et urethrae and the rectum. Insertion is on the fourth and fifth hemal arches and on one of the tendons which from these bones give rise to m. extensor caudae medialis.

M. ischiocaudalis (figs. 21, 41): This is a strong and fleshy mass which from its origin, by short tendinous fibers on the region of the ischiadic spine, spreads out toward the proximal part of the tail where it is inserted on the costal processes of caudal vertebrae 1 to 7. The ischiocaudalis is proximally covered by the gluteus maximus with the internal pudendal vessels and the pudendal nerve running between the two muscles along the origin of the first. Its deep surface is in relation with the pubo- and iliocaudalis and closes dorsally the narrow space of the ischiorectal fossa.

M. flexor caudae lateralis: I regard this long and segmentally arranged muscle as the homologue of m. flexor caudae longus of the rhesus monkey (Howell and Straus, 1933). Its fleshy fibers arise from (1) the last lumbar vertebrae and the disk just craniad to it, (2) the pelvic surface of the sacrum lateral to the sacral foramina and, in the tail, (3) the ventral aspect of the caudal costal processes or, in those more distal vertebrae where they have been lost, on (4) the cranial tubercle resulting from their modification. The insertion is by two groups of long tendons: (1) on the tip of the costal processes beginning at Cd 8 or 9 and continuing on the distal costal tubercle down to the end of the tail, and (2) on the ventroproximal sesamoids or tubercles beginning at Cd 8 or 9.

M. flexor caudae medialis: This is the homologue of m. flexor caudae brevis as described in the rhesus macaque by Howell and Straus (1933), but I prefer to name it differently because of its presence throughout the tail and sacral regions. It arises by fleshy fibers from (1) the pelvic surface of the sacrum medial to the sacral

foramina, (2) the body of all the caudal vertebrae, and (3) the corresponding hemal arches or sesamoids. It is also serially arranged. One given segment forms a powerful long tendon which approaches the midline to be inserted on the sesamoids or tubercles of the sixth or seventh vertebrae away from its origin.

The first three caudal muscles are essentially the same in the southern howler where Sirena (1871) calls them pubococcygeus, ileococcygeus, and ischiococcygeus externus. The differences relate to their attachments, which he describes as being on hemal arches 2 and 3 for the first, 2, 3, and 4 for the second, and the transverse (costal) processes of Cd 2, 3, 4, and 5 for the last. The medial and lateral flexors of the tail in the two species of howler are likewise similar.

Nerve supply of the caudal group.—The pubo- and iliocaudalis are innervated by a common branch from the ventral ramus of S III (fig. 35). The nerve to the ischiocaudalis is formed by contributions from Cd I and S I (fig. 35). The medial and lateral flexors of the tail are innervated by ventral rami of the caudal nerves.

Function of the caudal group.—Flexors and abductors of the tail.

Comparative anatomy of the caudal group.—*Brachyteles* (Hill, 1962) appears to have an arrangement similar to that of the two species of howlers. I suspect that the same is true also for the remaining prehensile-tailed monkeys.

Ventral Group

M. sternohyoideus: This paired muscle lies at each side of midline enclosed within the more superficial lamina of the fascia of the infrahyoid muscles. It extends from the thorax to the hyoid bone (fig. 3) and originates from (1) the deep aspect of the first two costal cartilages over their sternal half, (2) the corresponding chondrosternal joints, and (3) adjacent sternal pieces. The fleshy bundles ascend into the neck medial to each costothyroideus with which they cover the sternothyroideus. The sternohyoideus attains its maximum width in front of the swollen thyroid cartilage past which, in front of the thyrohyoid membrane, it narrows down a little but not so much as at the origin. Insertion is along the lower subcircular margin of the apertura bullae hyoideae. The attachment at each side of the midline extends from the midpoint to the very much reduced hypohyal. A triangular space whose base corresponds to the incisura sternalis separates the sternohyoideus of each side below the prominence of the thyroid cartilage. The two muscles come together along the midline in front of the thyrohyoid space and appear to form here a single sheet. Lampert (1926) and Sirena (1871) noted also the strong

development of this muscle. The last author and Sandifort (1834) remarked that its transverse dimension was reduced from above downward.

Nerve supply: The sternohyoideus receives two branches, one given off either from the descendens hypoglossi, or the ansa, goes to the upper part of the muscle, the other reaches the distal part and is either a branch or the continuation of the long ramus of the ansa hypoglossi to the sternothyroideus (fig. 23).

Function: Its contraction should displace the hyoid away from the mandible, and together with the stylohyoideus it must help to close the hyolaryngeal canal by pressing the bulla against the epglottis. By acting on the thyroid plates the sternohyoideus probably helps to empty the saccules.

M. sternothyroideus: It lies under cover of the sternohyoideus and against the isthmus of the thyroid gland, the cricoid arch and m. cricothyroideus. The deep lamina of the infrahyoid fascial layer provides a cover for the sternothyroideus. Origin is by fleshy bundles attached inside the thorax to (1) the medial end of the third costal cartilage, sternocostal articulation and adjacent sternal pieces and (2) the same regions at the level of the second cartilage below the origin of m. sternohyoideus. The fleshy band ascends into the neck immediately in front of the internal thoracic artery and other superior mediastinal structures. It is inserted on the distal border of the thyroid cartilage near the root of the lower horn (fig. 3). Sirena (1871) describes the origin only from the second costal cartilage and adjacent sternal surface. Lampert's account (1926) of this muscle in the howler does not include the origin because the specimens he studied had all been beheaded. Sandifort (1834) points out how the ending of the sternothyroideus on the thyroid cartilage does not cause any inferior tubercle or linea obliqua. Starck and Schneider (1960) regard this muscle as formed by two portions, one corresponding to the structure I have just described, the other to the costothyroideus.

Nerve supply: Distal twigs from the long branch of the ansa hypoglossi (fig. 23).

Function: Depressor of the thyroid cartilage.

M. costothyroideus: This is a ribbon-like muscle found on the lateral aspect of the larynx (fig. 3) and within the same fascial cover as the sternohyoideus. It is broader at its insertion and begins by muscular fibers from the deep surface of the lateral half of the first and second costal cartilages. Near the origin the ventral border of the costothyroideus is very near the lateral border of m. sternohyoideus and the two muscles appear to form a single sheet for a short distance. They separate by following different directions and leave a space in between through which the thyrohyoideus becomes super-

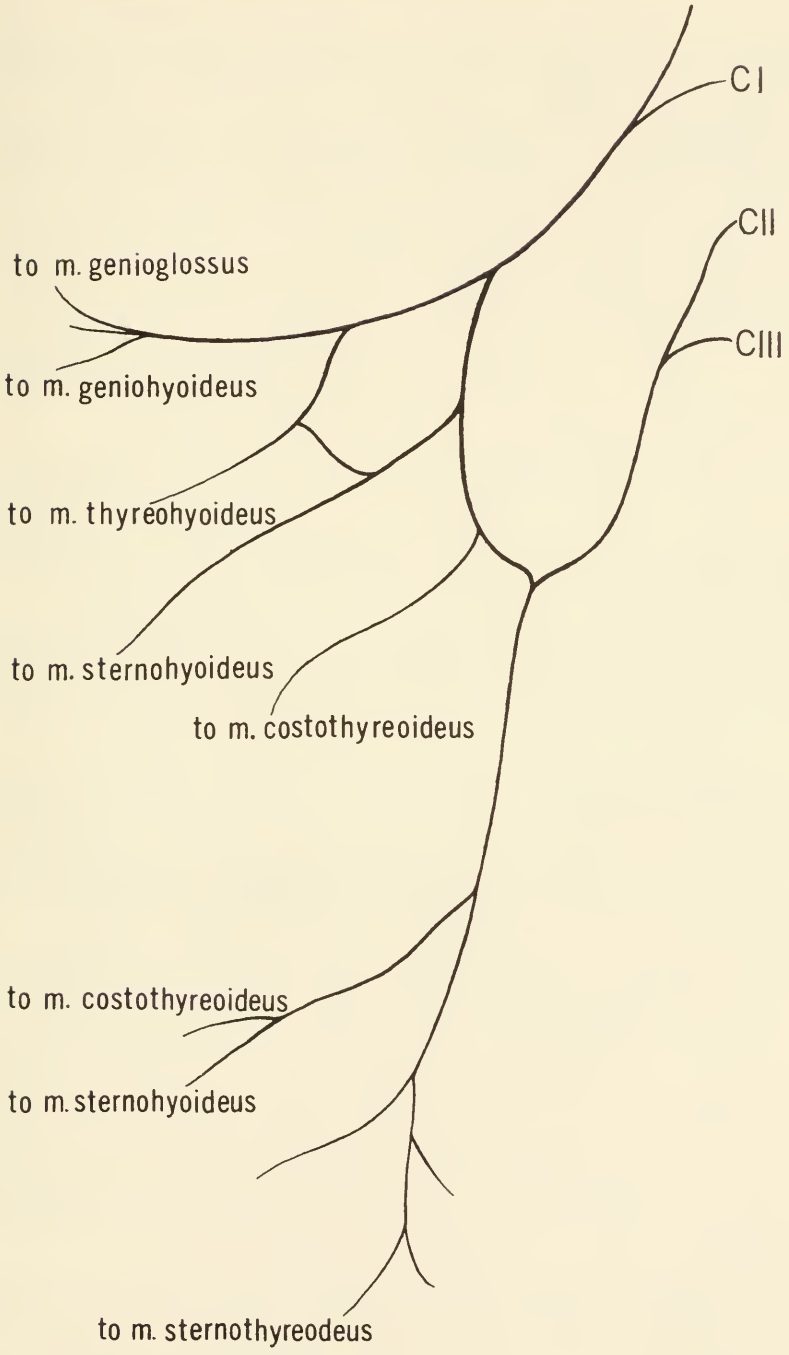

FIGURE 23.—Innervation of ventral trunk muscles in the left side of the neck, male specimen.

ficial. As the muscle approaches the upper border of the thyroid plate the dorsal fibers of the now much broadened thyrohyoideus override the anterior fourth of the costothyroideus. It ends on the outer lip of the upper thyroid border along its rear third and by its deeper fibers on the adjacent part of the external surface of the plate. Sandifort (1834) and Sirena (1871) described an intermediate tendon in the muscle. The latter author gives only the first rib and costal cartilage as points of origin. Hill (1962) believes that this muscle replaces the omohyoideus. The interpretation of Starck and Schneider (1960) was given in the section dealing with m. sternothyroideus.

Nerve supply: It is commonly supplied by two branches of the ansa hypoglossi, an upper one given off the ansa and a lower from the long descending ramus to the sternohyoideus (fig. 23).

Function: In combination with the sternothyroideus it retracts the thyroid cartilage against the cricoid and trachea. It is conceivable that the contraction of the two costothyroideus muscles will spread the upper margins of the plate out and downward. The thyrohyoid space and that circumscribed between the thyroid cartilage and the epiglottis will thus be enlarged and a vacuum created within the saccules and the hyolaryngeal canal, which will be immediately invaded by an inrushing column of air. In this manner the antrum of the bulla is also filled with air and the vibrations of the soundproducing structures can reach these chambers to be amplified.

M. thyrohyoideus: This muscle, the cranial continuation of m. sternothyroideus (fig. 3), arises from the posterior third and outer lip of the lower thyroid margin. Its superficial fibers are continuous with those of the sternothyroideus. The flattened belly covers the thyroid attachment of the inferior pharyngeal constrictor and lies initially under the costothyroideus. The thyrohyoideus expands when crossing the upper thyroid margin and its dorsal fascicles now cover the terminal part of the costothyroideus. Insertion is by fleshy fibers on (1) the proximal hyoid part of the cornu branchiale I and (2) the tentorium bullae between the hypohyal and the cornuhyoid joint. The muscle is broader at its insertion than at the origin, the proportion being about 2:1. The findings of other authors (Lampert, 1926; Sandifort, 1834; Starck and Schneider, 1960) do not differ from mine.

Nerve supply: It is usually supplied by a branch of the hypoglossus nerve, but it may also be innervated directly from the descendens hypoglossi or from a small ansa between cranial nerve XII and the upper branch to the sternohyoideus (fig. 23).

Function: Contraction of this muscle draws the cornu branchiale I toward the upper border of the thyroid cartilage. At the same time it presses against the flexible wings of the plate. A squeezing action can then be exerted on the saccules contained in front of the epiglottis

in the thyrohyoid space. The air that had been drawn into these membranous structures will then be blown back into the air passage.

M. geniohyoideus: This strong and paired muscle has origin by short tendinous fascicles from the basis mandibulae at each side of the midline (fig. 5). The attachment is frequently marked by corresponding bony flanges. The fibers are dorsally directed toward the laterolingual surface of the bulla hyoidea where they insert over an extensive area (fig. 7). Fatty masses separate the muscle from the overlying genioglossus and the anterior part of the mylohyoideus covers it in the submandibular triangle. The descriptions of this muscle by Lampert (1926), Sandifort (1834), Sirena (1871), and Schön (1964a) do not differ from the present one.

Nerve supply: The XII cranial.

Function: It pulls on the bulla thus allowing for the opening of the thyrohyoid canal. This role was discussed in a previous communication (Schön, 1964a).

Comparative anatomy: Campbell (1937) reported the absence of an omohyoid in *Lagothrix*, *Ateles*, and *Alouatta*, but since his study was not particularly concerned with the neck, I am not able to determine if that muscle is replaced by a costothyroideus in any of these two genera besides the howler. Lampert (1926) could not differentiate an omohyoideus at the point of insertion in the spider monkey, but indicates its presence in the woolly monkey. The fact that Lampert's observations were done mainly in neck organs and not always in complete specimens should be considered in evaluating his results. Hill (1962) says that an omohyoid is absent in *Brachyteles* and does not indicate the presence in this animal of a muscle that could be identified with the costothyroideus. M. omohyoideus was found in *Cebus* (Campbell, 1937). Lampert (1926) does not describe the muscle in his specimen of this genus, but mentions the relations of m. sternothyroideus with it. I therefore assume that the capuchin monkey has such a muscle. The most relevant difference between *Alouatta* and the other prehensile-tailed ceboids in relation to all these muscles is one of size. They attain a prominent development in the howler monkey parallel to the increase in proportions of the hyolaryngeal apparatus. Otherwise, no major divergences can be pointed out except to say that the superficial fibers of the sternothyroideus do not pass up to continue with those of the thyrohyoideus in *Lagothrix* (Lampert, 1926).

M. rectus abdominis: A long, ventrally compressed, paired muscle lying at each side of the midline between the thorax and the pubis. It arises by thin but resistant musculotendinous digitations from the ventral surfaces of the highest costal cartilages (1–6 in one 13-rib male, one 14-rib male, one female; 2–6 in the other 14-rib male where

the slip from the fifth was symmetrically absent). Origin from costal segments two to five is lateral to that of the pectoralis minor, but digitations from the sixth reach the midline. The broad muscular band formed at the lower and ventral border of the rib cage narrows progressively on approaching the pubis. It is inserted on the symphysis and crest behind the falx inguinalis. The muscle has no transverse serrations and the pyramidalis is absent. The costal attachment in *Alouatta fusca* (Sirena, 1871) on ribs 1–6 and the xiphoid process is not essentially different from the situation in my 13-rib males.

Nerve supply: Twigs from the anterior cutaneous branches of the lower five thoracic, all of the thoraco-abdominal and the subcostal nerves.

Function: It is similar to that already assigned to the broad abdominal muscles in previous paragraphs.

Comparative anatomy: The rectus abdominis appears to offer no major difference among these animals. The wide variability observed in relation to the formation of the rectus sheath has been mentioned in connection with the lateral hypaxial group.

M. diaphragma (fig. 20): This is an extensive musculotendinous partition transversely placed between the cranial third and caudal two-thirds of the trunk. The diaphragm is deeply concave on its abdominal side forming a high dome over the abdominal viscera, mainly the liver. The highest part corresponds to its center in agreement with the large development of the left hepatic lobe. There is a kidney-shaped tendinous center whose convex ventral margin lies close to the thoracic wall, while its posterior concave border is far from the dorsal body wall. All fibers of the muscle end on this central tendon. The diaphragm arises ventrally from the inner surface of the thoracic outlet formed by the cartilages of the seventh, eighth, and ninth ribs. There is a small hiatus behind the xiphoid process, but it does not reach the central tendon. Dorsally, and at the midline a pair of crura are formed in front of the upper lumbar vertebrae. A tendinous right crus arises from the intervertebral disks between L 3 and L 4, and L 2 and L 3, as a continuous band next to the anterior longitudinal ligament. The left crus has a similar origin but lies sinistral to the ligament and is thinner. Muscular fibers prolong these tendinous columns and are directed toward the concavity of the central tendon. The crura expand cranially encircling the aorta and the esophagus. A musculotendinous band joins the crura and separates the vascular from the digestive tube. Digitations are contributed to the diaphragm from the costal processes of L 1 and L 2 and from the last four or five ribs. A costodiaphragmatic sinus can be recognized between the slips from the first lumbar and the last rib. I could not identify any arcuate ligament as such because none of these dorsal

digitations are connected by ligamentous fibers. The diaphragm was not described by Sirena (1871).

Nerve supply: Right and left phrenic nerves. Twigs were seen reaching the muscle from the subcostal nerves.

Function: Respiration.

Comparative anatomy: The diaphragm of *Ateles* is regarded by van den Broek (1908) as possessing a central tendon larger than in any other platyrrhine and shaped very much like that of man. Winckler (1926) studied the crura in several mammals and found the right crus of the spider monkey larger than the left, arising by two fascicles from the ventral aspect of the sixteenth and eighteenth thoracolumbar vertebrae. The two crura met in front of the eighteenth body where they were firmly anchored and fused with the fibers of the anterior longitudinal ligament. Winckler (1926) does not give the number of rib-bearing vertebrae in his specimen. If we take 15 as the most representative value for *Ateles* (see Schultz and Straus, 1945), the origin of the crura in this genus could be assigned to the second and fourth lumbar vertebrae and, therefore, regarded as not too different from the situation in the howler. The right crus in *Brachyteles* (Hill, 1962) is also the larger, arising as far as L 3, whereas the left comes from L 1 and 2. Hill (1962) describes a xiphosternal origin in this animal.

Muscles of the Upper Extremity

Dorsal (Extensor) Musculature

Shoulder Girdle Group

EXTRINSIC SERIES

M. atlantoscapularis anterior (fig. 16): This muscle extends between the atlas and the shoulder girdle. Together with m. trapezius it forms the dorsal border of the narrow posterior cervical triangle. Tendinous fibers arise from the transverse process of C 1, lateral to and partially overlapping the origin of the scalenus medius (reinforcing bundle). These fascicles change shortly into a muscular belly which spreads out toward the shoulder and crosses the distal half of the craniolateral margin of the trapezius. Insertion is on the lateral half of the clavicle, the acromioclavicular capsule, and the upper surface of the acromion, always between the attachments of m. deltoideus and the trapezius (fig. 24).

The atlantoscapularis anterior of the red southern howler corresponds to that of my description. Sirena (1871), nevertheless, adds that there is an aponeurotic expansion between the muscle and the

angle of the mandible. I did not notice any particular thickening of the superficial cervical fascia that would merit a separate description. Campbell (1937) studied the shoulder muscles in several platyrrhines, including one *Alouatta palliata*. The muscle in the Central American species does not offer any difference. It also is inserted superficial to m. trapezius, but is slightly subdivided distally into two bellies. Hill

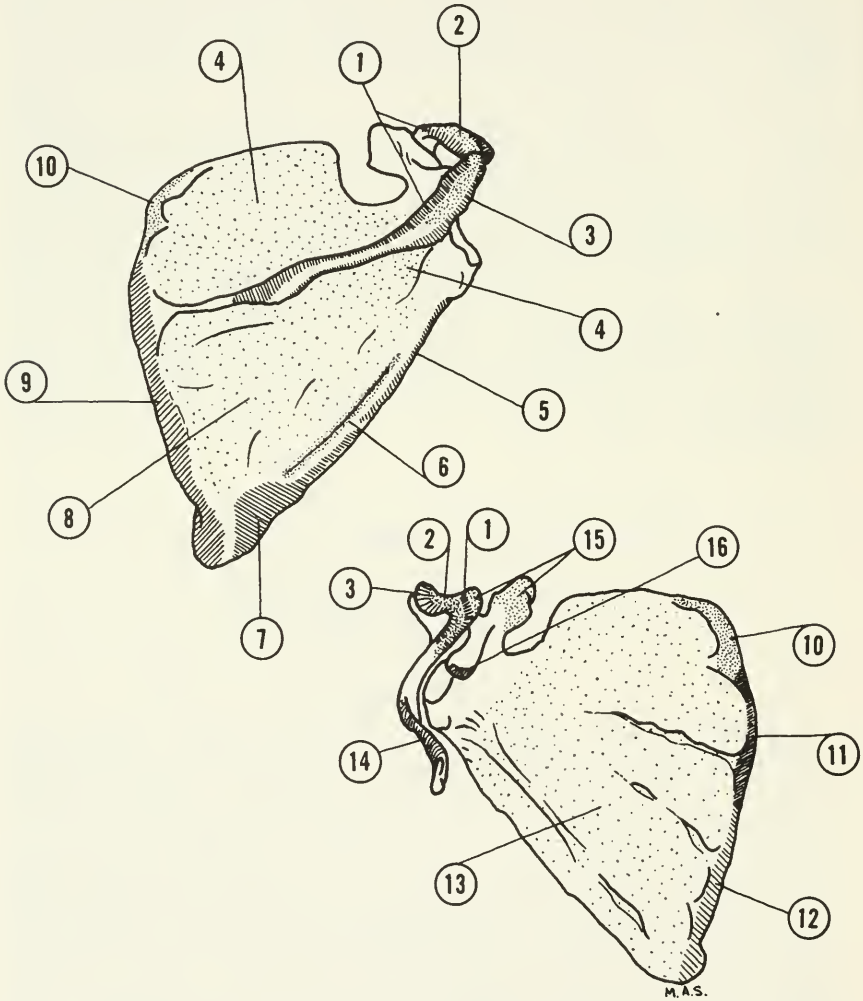

FIGURE 24.—Muscular attachments of the scapula (1, m. trapezius; 2, m. atlantoscapularis anterior; 3, m. deltoideus; 4, m. supraspinatus; 5, m. triceps, caput longa; 6, m. teres minor; 7, m. teres major; 8, m. infraspinatus; 9, m. rhomboideus; 10, m. atlantoscapularis posterior; 11, m. serratus anterior, pars cranialis; 12, m. serratus anterior, pars caudalis; 13, m. subscapularis; 14, m. pectoralis major; 15, m. subclavius; 16, m. biceps brachii, caput breve).

(1962), apparently following Sirena (1871), also describes the aponeurotic expansion to the mandible, but he regards this variation as part of the muscular origin. Ashton and Oxnard (1963) studied one howler, *Alouatta sp.*, in their monograph on the shoulder muscles of the primates. The atlantoscapularis anterior in this individual coincides with that of the three species already alluded to but, in addition, more closely resembles the Central America variety in having two heads of insertion, one attached to the acromion, the other to the clavicle.

Nerve supply: A branch from the anterior division of either C III or IV.

Function: It elevates the shoulder.

Comparative anatomy: The acromioclavicular insertion of *Alouatta* is always superficial to that of m. trapezius (fig. 24). This arrangement is also found in *Lagothrix* (Ashton and Oxnard, 1963; Campbell, 1937; Miller, 1932; Robertson, 1944) and *Ateles* (Campbell, 1937; Miller, 1932; Schück, 1913b). Ashton and Oxnard (1963) report one specimen of the spider monkey where the ending of m. atlantoscapularis anterior lies deep to that of the trapezius. This insertion is always deep to m. trapezius in *Cebus* (Campbell, 1937; Miller, 1932, Schück 1913b). It is also in the howler, *Ateles*, and *Lagothrix* that the shoulder attachment of the muscle constantly includes the acromion and the clavicle (Ashton and Oxnard, 1963; Campbell, 1937; Miller, 1932; Schück, 1913b). This is not the case for the ring-tailed monkey where its insertion is restricted to the acromion and/or the spine (Campbell, 1937; Miller, 1932; Schück, 1913b). Hill (1962) does not describe the insertion of the trachelo-acromialis (m. atlantoscapularis anterior) in the shoulder of *Brachyteles*. The distal division of the atlantoscapularis anterior into two heads, one for the clavicle and the other for the acromion, has been found in only two howlers, one *Alouatta palliata* (Campbell, 1937) and one *Alouatta sp.* (Ashton and Oxnard, 1963). It also occurs in two *Ateles* (Campbell, 1937; Schück, 1913b), but apparently never in *Cebus* or *Lagothrix*.

The muscle of the howler conforms in its origin, insertion, and general arrangement more with the three brachiators than with the versatile capuchin monkey.

M. atlantoscapularis posterior (figs. 17, 19, 25): This muscle was constantly present as a fleshy band extended from the transverse process of the atlas to the cranial angle and upper part of the spinal border of the scapula. Origin is from the tip of the first cervical transverse process. Its belly descends caudolaterally in contact with the first digitation of serratus anterior, pars cranialis. As it approaches the scapula it expands and is inserted on the cranial half of the supraspinous part of the scapular vertebral border up to the cranial angle (fig. 24). This ending invades both surfaces of the bone near the

margin. The muscle is contained together with the anterior serratus within a common aponeurotic covering which is very resistant to the point of making difficult their separation.

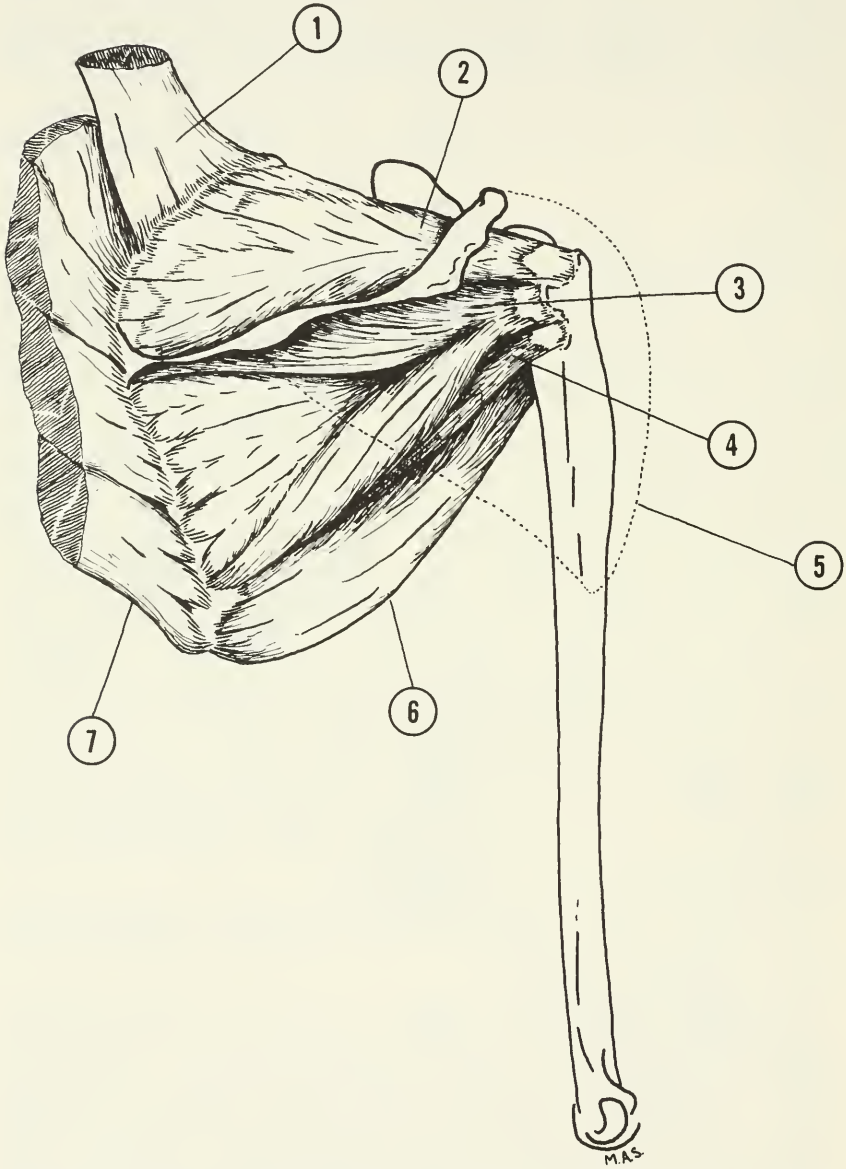

FIGURE 25.—Dorsal view of the shoulder (1, m. atlantoscapularis posterior; 2, m. supraspinatus; 3, m. infraspinatus; 4, m. teres minor; 5, m. deltoideus (contour); 6, m. teres major; 7, m. rhombiodeus).

Sirena (1871) describes this muscle together with the pars cranialis of serratus anterior and calls them m. levator anguli scapulae. It is clear from his text that the higher digitation of this levator corresponds to the muscle I have just studied in *Alouatta seniculus*. He apparently did not see any separation that would justify their independent treatment. Ashton and Oxnard (1963) have also included one such muscle with the serratus anterior, pars cranialis, in their single howler specimen. Yet it is clear from their text that an atlantoscapularis posterior, as I have interpreted it, is also present in this case. Campbell (1937) does not separate this muscle from the serratus anterior in *Alouatta palliata*. I do emphasize the distinctness of the two muscles on the basis of the peculiar scapular attachment of the first in my red howlers, where its fascicles are fixed to both lips of the cranial half of the supraspinous portion of the vertebral border (fig. 25). This arrangement is very evident on plate 3, figure 12, of Ashton and Oxnard's (1963) study. Otherwise, the atlantoscapularis posterior can hardly be separated from the serratus anterior, pars cranialis. This emphasis of mine will be further explained when I deal with the functions of the muscle.

Nerve supply: A branch from the anterior division of C III.

Function: It elevates the scapula. In addition, I think that when the scapula is fixed the muscle is an accessory extensor of the neck. By such an action it produces, together with the rhomboideus, an extra traction upon the margin of the bone, and to this influence the scapula has responded with an enlargement of the corresponding portion of its vertebral border. The extraordinarily large supraspinous fossa in *Alouatta* is a character already indicated by several authors (Erikson, 1963; Hill, 1962; Schultz, 1930). I do not know if this character occurs also in the very young howlers where the hyolaryngeal apparatus has not yet attained its maximum size.

Comparative anatomy: The atlantoscapularis posterior is an independent muscle in one *Ateles* and two *Lagothrix* (Campbell, 1937; Robertson, 1944) in all of which it arises only from C 1. Schück (1913b) describes its origin from C 1, 3, and 4 in another spider monkey. It arises from C 1–4 in *Brachyteles* (Hill, 1962), where the muscle is described as different from the serratus anterior. In all other spider and woolly monkeys reported (Campbell, 1937), it forms a single muscular plate with the serratus.

In general, the muscle tends to be fused with the serratus anterior, pars cranialis, in all the five genera under consideration; but it appears as if in *Alouatta* it might be responsible for the large supraspinous fossa due to its possible function of extending the neck in this animal.

M. trapezius: This is a triangular muscle extending from the occiput and midline of the cervical and upper thoracic regions to the

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shoulder. In the skull the lambdoid crest and the external occipital protuberance are well developed in adult males. The cranial origin of the trapezius is by fleshy fibers from the medial half of the nuchal crest and the external occipital protuberance in five specimens (fig. 5). In the neck and high thoracic region, it arises from the nuchal ligament, the spine of C 7, the spines of the upper thoracic vertebrae (the distribution in five specimens was down to T 7 in two, to T 8 in two, and down to T 9[1] in one), and from the intervening supraspinal ligaments. Most of these fibers are fleshy; only those from the last cervicals and first thoracic are aponeurotic and form with the trapezius of the other side a speculum rhomboideum. The lower thoracic fibers have a short tendinous origin. Occipital and higher cervical bundles pass caudolaterally to insert on the outer half of the clavicle, the acromioclavicular capsule and upper surface of the acromoin (fig. 24). This attachment and the lower half of the lateral border of the trapezius are covered by the atlantoscapularis anterior as this ends on the acromion and clavicle. Intermediate fibers are transversely oriented toward their insertion on the cranial border of the scapular spine. The distal fascicles of the trapezius are directed laterocranially, ending by a short aponeurosis on the medial half of the spine. The muscle is thicker in the cervical than in the thoracic region. According to Sirena (1871), the cranial origin in *Mycetes fuscus* (=*Alouatta fusca*) is only from the medial third of the superior semicircular line and in the vertebral column it reaches T 8.

Nerve supply: Cranial nerve XI after it receives a communicating branch from C II.

Function: It elevates the shoulder and, as discussed by Oxnard (1963), plays an important part in bringing the glenoid angle of the scapula upwards.

Comparative anatomy: From a perusal of the available literature (Ashton and Oxnard, 1963; Campbell, 1937; Hill, 1960, 1962; Miller, 1932; Sirena, 1871), it becomes apparent that the origin of the trapezius along the lambdoid crest is larger in the howler than either the spider, woolly, or capuchin monkeys. Data on *Brachyteles* (Hill, 1962) suggests a similar extensive origin in this genus. With respect to this character, the howler stands apart from the condition of quadrupeds and the other semibrachiators as described by Ashton and Oxnard (1963), but aligns itself with the last in having a thicker cervical than thoracic part of the trapezius and an insertion for this muscle reaching farther out in the shoulder into the clavicle. I regard the wide occipital origin of the trapezius in *Alouatta* as perhaps related to the possible role of the muscle in helping to hold the head up against the influence exerted by the presence of the heavy hyolaryngeal apparatus in the

[1] Observation in an additional young adult male.

neck. That voice-producing organs have affected other details of the occipital region, in particular those of the cranium, has been shown by the studies of Biegert (1963) and Leche (1912).

M. serratus anterior (fig. 17): This is a broad muscular sheet connecting the vertebral border of the scapula to the ribs and the lower six cervical vertebrae. It is divided into a pars cranialis and a pars caudalis separated by a narrow and long hiatus through which the scalenus medius reaches its insertion. Pars cranialis arises by (1) fleshy digitations from the posterior tubercles of C 2 to C 7 between the origin of the scalenus posterior in front and the insertion of the longissimus behind, and (2) as two muscular bands from the outer surface of the bodies of ribs 1 and 2. The vertebral and costal portions are separated by a short hiatus through which the deep cervical artery reaches its position between the semispinales muscles. A more or less continuous belly is thus formed whose fibers pass towards the scapula. Costal fascicles are less oblique than the others. Insertion takes place on the ventral lip of the vertebral border of the blade but only over (1) the caudal half of its supraspinal part and (2) the cranial fourth of its infraspinal part (fig. 24). Pars caudalis is formed by six fleshy flat bundles arising from the outer surface of the body of the third to eighth rib on the lateral aspect of the thorax where they alternate with those of m. obliquus externus abdominis and the latissimus dorsi. These digitations join, not too far after their origin, into a single sheet. Fibers from the lower ribs are more oblique in direction. Insertion is on the remaining of the vertebral margin down to the caudal angle. The pars caudalis of the muscle is a bit more robust and longer than the cranialis.

As explained before, Sirena (1871) treats the pars cranialis as forming with the atlantoscapularis posterior a single muscle, the levator anguli scapulae. The serratus has origin, according to him, only on the upper nine ribs and insertion along the entire vertebral border of the blade. He points out that the muscle is thin near the upper angle, probably with the idea of contrasting this condition with what appears to have been a thicker caudal portion. Campbell (1937) explains that the muscle in *Alouatta palliata* is divided by the insertion of the long scalene (m. scalenus medius). The proximal portion of this species arises from all cervical vertebrae and the first two ribs. The distal extends caudally, but he does not say how far down into the thorax.

Nerve supply: The pars cranialis receives branches from the ventral rami of C II, IV, and V; pars caudalis is innervated by the long thoracic nerve and this is usually formed by contributions from C VI to VIII (fig. 26).

Function: Both parts of the muscle should act as stabilizers of

the scapula and the caudalis is probably important also in respiration. Its moderate robustness suggests that the role of the serratus anterior in laterally rotating the lower scapular angle, as in raising the shoulder, is still of some significance in the howler, but the wideness of that angle and its short distance from the center of rotation of the bone indicate that this mechanism might not be a very efficient one in the animal.

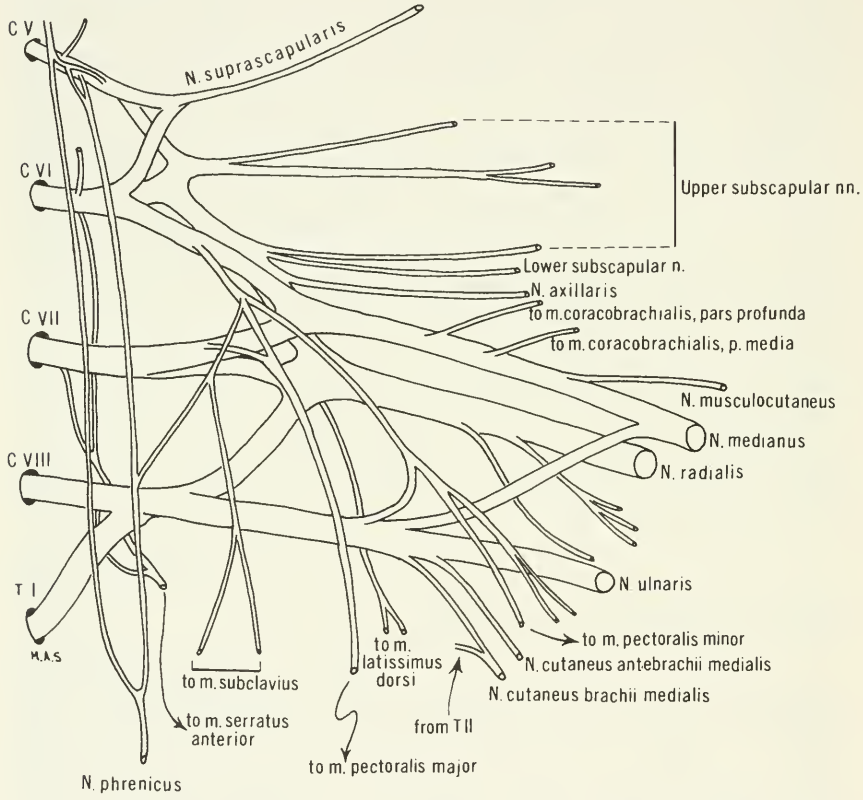


FIGURE 26.—Plexus brachialis as observed in the left side of one male.

Comparative anatomy: The division of the muscle by the scalenus medius is a constant feature in *Alouatta* (Ashton and Oxnard, 1963; Campbell, 1937; this report), *Ateles* (Ashton and Oxnard, 1963; Campbell, 1937; Hill, 1962), *Lagothrix* (Campbell, 1937; Hill, 1962) and *Cebus* (Campbell, 1937; Schück, 1913b). Hill (1962) reports it also for the woolly spider monkey. *Cebus* (Schück, 1913b), *Lagothrix* (Campbell, 1937) and the howler appear to have a rather uniform pars cranialis arising from the lower six cervical vertebrae and cranial ribs. On the other hand, the origin from C 2 is absent in

Ateles (Schük, 1913b), and that from C 5 in *Brachyteles* (Hill, 1962). With regard to the number of digitations which form the pars caudalis, it is interesting to note that the six slips of the howler align this genus with the quadrupedal group rather than with the semibrachiators of Ashton and Oxnard (1963). Unfortunately, there are no data that would allow us to compare, even if only in a qualitative manner, the differential degree of development of pars cranialis versus its caudal counterpart in the genera we are considering. Such information might permit us to evaluate the relative functional importance of each of them. *Alouatta*, with a not too powerful caudal portion in relation to the cranial, appears in position intermediate between the semibrachiators and quadrupeds of Ashton and Oxnard (1963).

M. latissimus dorsi: This is a broad, flattened muscular sheet covering the dorsolateral aspect of the thorax and extending from the vertebral column and lower ribs to the humerus. Of roughly triangular shape, its base corresponds to the dorsal midline and caudal part of the thorax, the apex to the axilla. The upper border is nearly horizontal and the lateral obliquely directed toward the insertion. The origin is double: (1) Strong tendinous fibers arise from the spinous processes of T 7 down to L 1 or 2. They form a continuous aponeurotic lamina intimately joined to the thoracolumbar fascia (fig. 12). (2) Fleshy digitations begin in ribs 8–12 in one 14-rib male, 7–11 in a 13-rib male, 9–12 in the other 14-rib male, and 8–11 in the 13-rib female. On reaching the floor of the axilla the muscular elements form a strong flat tendon and are tightly bound to m. teres major by connective tissue. The highest fibers of the latissimus pass along the dorsal border of the tendon, those from the lower ribs continue on its ventral edge. Insertion is at the bottom of the broadened sulcus intertubercularis. This ending does not impress a fossa on the bone, but as in the case of *Ateles* (Napier and Davis, 1959; Schön, 1965) and also in *Cebus* (Schön, 1964b), the groove for the muscular ending is broad and its caudal limit ill-defined.

Sirena (1871) found the muscle arising by four fleshy digitations from ribs 9–12 in all his three specimens. He describes the spinal origin as reaching T 6 by means of an aponeurotic lamina fused with the thoracolumbar fascia. The cranial origin in *Alouatta palliata* is T 7 (Campbell, 1937) and its highest costal slip comes from rib 7 or 8.

Nerve supply: The thoracodorsal nerve, arising from the posterior cord of the brachial plexus (fig. 26).

Function: The muscle retracts the forearm and rotates it medially. Its main function, nevertheless, is that of propelling the body (Ashton and Oxnard, 1963). The not too strong development of the latissimus in the howler indicates that it does not play a very active part in propelling the body from above.

Comparative anatomy: The latissimus dorsi of the howling monkey presents a condition intermediate between that of *Cebus* on the one hand and *Ateles* on the other. In its mild development, it is reminiscent of the situation in the capuchin monkey; but in the direction of its fibers the resemblance is with *Ateles*. The number of costal digitations, an average of four for a total of seven specimens (three of Sirena (1871), four mine), is intermediate between *Cebus* and the spider monkey. Schück (1913a) reports three specimens of the first genus with three, four, and seven slips, respectively. The first three digitations of the animal with seven were rather weak. Campbell (1937) found only two in one *Cebus capucinus*. Schück (1913a) indicates six digitations in one *Ateles ater* (=*Ateles paniscus*). Hill's coverage (1962) of the latissimus in *Brachyteles* suggests that there might be six in this animal. The situation for *Lagothrix* is not clear, as the only source about this muscle is Campbell (1937), and he says merely that the highest costal origin for latissimus is the eighth rib. The caudal migration of the latissimus origin toward the iliac blade has not gone as far in *Alouatta* as in *Ateles*. It stops on the 12th (five 14-rib specimens) or 11th (two 13-rib specimens) rib in the first genus, but in the second genus Schück (1913a) describes it as taking place by six slips from ribs 9 to 14. The close association of this muscle with the teres major has been reported also in all the other genera, but only Campbell (1937) has found a true origin for the latissimus from the inferior angle of the scapula.

M. rhomboideus (fig. 25): This is a strong muscle found deep to trapezius in the neck and upper thoracic regions. Its undivided and flattened belly occupies the space between the vertebral border of the scapula, the occiput, and the spines of all the cervical and upper four vertebrae. Origin is by fleshy and thick bundles from (1) the medial two-thirds of the lambdoid crest and the protuberantia occipitalis externa, between the origin of m. trapezius superficially and the insertion of the splenius deeply (fig. 5); (2) the ligamentum nuchae; and (3) the spines of C 7 to T 4 and the associated ligamenta supraspinalia. In the left side of one male the cranial origin was limited to less than one-fourth of the lambdoid crest adjacent to the protuberance. Occipital and cervical fibers form the thicker part of the muscle, those extending from the cranium to the scapula are nearly vertical, the rest increasingly oblique but never attaining a horizontal direction, even in the thorax. The muscle is thicker near its insertion, which is on the dorsal lip of the vertebral border from the caudal angle up to about the middle of the supraspinous part of the margin (fig. 24).

A comparison of this muscle with that of *Alouatta fusca*, as described by Sirena (1871), reveals no difference. According to him, the occipital

attachment extends over the lateral three-fourths of the superior nuchal line. Hill (1962) specifies T 4 as the last vertebrae of origin in the spine. Campbell (1937) also notes the extensive occipital attachment in relation to the nuchal crest. Furthermore, he remarks that the rhomboideus capitis is present but fused to the rest of the muscle. Ashton and Oxnard (1963, pl. 3, fig. 12) attribute only a short origin to the muscle from the superior occipital line in semibrachiators including *Alouatta*, but their specimen of this genus suggests that the muscle possesses, in fact, a more extensive origin.

Nerve supply: The rhomboideus receives its innervation from the ventral rami of C III and IV. I never found it supplied by branches of the brachial plexus.

Function: Besides its action as a stabilizer of the shoulder, the rhomboideus appears to have importance in maintaining the head and neck extended. This function would be accomplished by the occipital and higher cervical fibers.

Comparative anatomy: In both *Cebus* (Campbell, 1937; Schück, 1913b) and the howler (Campbell, 1937; Sirena, 1871; this report) the rhomboideus is undivided and forms a continuous muscular lamina between the scapula, the occiput, and the spine. According to Schück (1913b), its caudal extension reaches T 6 in the capuchin. Campbell (1937) appears to have found variability in this genus because he says it is T 5 in one place and a few lines further states it to be T 7. Schück (1913b) explains, in addition, that the origin in *Cebus* from the linea occipitalis is very thin. This obviously contrasts with the strong appearance in *Alouatta*. M. rhomboideus is divided in *Ateles* (Schück, 1913b; Campbell, 1937). One portion is represented by a slender band springing from the lateral part of the nuchal crest; the rest and larger portion comes from the spines between C 6 and T 7 (Schück, 1913b). Hill (1962) describes in *Brachyteles* a rhomboideus minor with origin from the midcervical region of the ligamentum nuchae and the rhomboideus major reaching the spine of T 6. The subdivision of the muscle is also found in *Lagothrix* (Campbell, 1937), and Robertson (1944) describes a *rhomboideus dorsi* reaching T 4 or 5, a *cervicis*, and a *capitis* in this genus. The last is formed by two parts which merge after their independent origin.

INTRINSIC SERIES

M. teres major (fig. 25): Its robust and round belly is fixed by fleshy fibers to the caudal angle and the lower half of the axillary scapular margin (fig. 24). Its own sheath also affords origin to several fascicles. The voluminous belly passes toward the floor of the axilla with the latissimus tendon spiraling around it. On approaching the humerus, teres major changes into a frontally compressed, broad,

and fleshy band whose insertion is by means of short tendinous fibers on the upper fourth of the medial margin of the humerus or buttress for the lesser tuberosity (fig. 27). The buttress for the lesser tuberosity and that for the humeral head remain separate in *Alouatta*, blending distally with the surface of the shaft as in *Ateles* (Napier and Davis, 1959; Schön, 1965) and *Cebus* (Schön, 1964b).

The muscle studied in *Mycetes fuscus* (=*Alouatta fusca*) by Sirena (1871) is similar and, apparently, the findings of Campbell (1937) in the Central American howler are also the same, as he does not stress any different character.

Nerve supply: The inferior subscapular nerve enters the muscle and probably receives fibers from C V and VI (fig. 26).

Function: A medial rotator and retractor of the humerus. It helps to propel the animal by this latter mechanism.

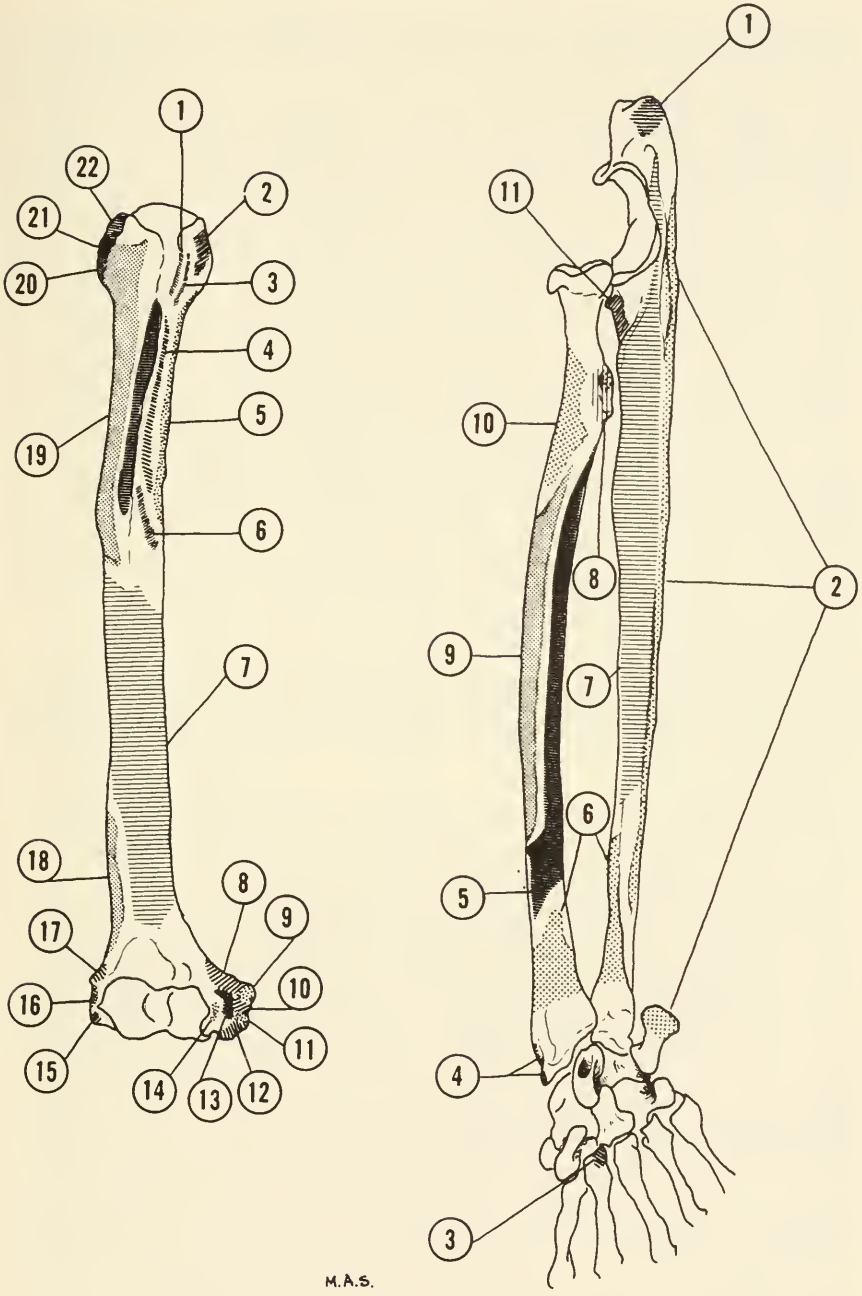
M. subscapularis (fig. 17): It is a powerful triangular muscle occupying in the scapula the whole extent of its costal surface except the marginal area along the vertebral edge and the neck (fig. 24). The muscle is formed by several bipennate bundles whose fibers originate from the three borders of the bone and from the surface of the fossa, which is marked off by transversely oriented crests intervening between broad grooves. Long but not very high tendinous septa are implanted on these ridges and provide additional origin. The pars axillaris of the subscapularis from the axillary sulcus is prominent. All the fibers converge toward the scapulohumeral joint in front of which they form a flattened tendon firmly connected to the articular capsule and inserted on the lesser tubercle (fig. 27).

Its arrangement in *Mycetes fuscus* (=*Alouatta fusca*) (Sirena, 1871) and *Alouatta palliata* (Campbell, 1937) is the same.

Nerve supply: Several subscapular nerves, superior and inferior, innervate the muscle. They all probably carry fibers from C V and VI (fig. 26).

Function: A strong medial rotator of the arm and stabilizer of the shoulder joint.

FIGURE 27.—Muscular attachments in the arm and forearm: *a*, Humerus (1, m. pectoralis abdominalis; 2, m. subscapularis; 3, m. coracobrachialis, pars profunda; 4, m. latissimus dorsi; 5, m. teres major; 6, m. coracobrachialis, pars media; 7, m. brachialis; 8, m. pronator teres; 9, m. flexor carpi radialis; 10, m. flexor digitorum superficialis, caput profundum; 11, m. palmaris longus; 12, m. flexor carpi ulnaris; 13, m. flexor digitorum superficialis, caput sperficiale; 14, m. flexor digitorum profundus, caput radiale; 15, m. extensor digiti quinti et quarti proprius (= extensor digiti minimi of N.A.); 16, m. extensor digitorum; 17, mm. extensores carpi radialis brevis and longus; 18, m. brachioradialis; 19, m. deltoideus; 20, m. teres minor; 21, m. infraspinatus; 22, m. supra spinatus); *b*, Radius and ulna (1, m. epitrochleo-anconeus; 2, m. flexor carpi ulnaris; 3, m. flexor carpi radialis; 4, m. brachioradialis; 5, m. flexor digitorum profundus, caput radiale; 6, m. pronator quadratus; 7, m. flexor digitorum profundus, caput ulnare; 8, m. biceps brachii; 9, m. pronator teres; 10, m. supinator; 11, m. brachialis.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M. deltoideus (fig. 25): This triangular muscle is formed by thick bundles which arise from the clavicle, acromion, and scapular spine and converge upon the humerus. Origin of pars clavicularis is by fleshy fibers from the lateral third of the collar bone below the attachment of the trapezius (fig. 24). Pars acromialis arises by muscular fascicles from the lateral edge of the acromion (fig. 24). Tendinous fibers forming a short aponeurotic pars spinalis arise from the lower lip of the posterior spinal (fig. 24) border and the infraspinal fascia. Pars spinalis was separated by a narrow cleft from the other two in both sides of one male. Acromial fibers are inserted on the proximal third of the humeral shaft between the deltopectoral crest and the lateral border of the bone (fig. 27). Its superficial fascicles become tendinous and attach more distally than the deep ones. Those from the clavicular and spinal parts converge upon the same area, ending on the bone and upon the tendinous elements of pars acromialis. Many deep fibers from the clavicle cross the deltopectoral interval and are fixed to the tendon of the pectoralis major. The area corresponding to the deltoid tuberosity is wide across the anterolateral surface of the humerus and extends proximally to the lower part of the greater tubercle.

Sirena (1871) explains how both m. trapezius and the deltoideus are interconnected through their attachment to the infraspinous aponeurosis. No difference can be noted in the same muscle studied by Campbell (1937) in *Alouatta palliata* and Ashton and Oxnard (1963) in *Alouatta sp.*

Nerve supply: A branch of the inferior division of the axillary nerve which seems to comprise fibers from C V and VI (fig. 26).

Function: Elevates the arm.

M. teres minor: This muscle is small when compared with those surrounding it. The teres minor is narrow but long and lies between the infraspinatus and teres major (fig. 25). Origin is by fleshy fibers from the dorsal lip of the axillary border where they occupy a narrow strip of bone between the origins of the two said muscles, but fall short of reaching either the angle or the neck of the scapula (fig. 24). Fibers are also contributed to the muscle from its investing sheath. All these fascicles have a bipennate arrangement and form a strong and round tendon after crossing superficial to the long head of the triceps. More laterally, the muscle adheres to the back of the scapulohumeral capsule and ends on the lower impression of the greater tubercle (fig. 27).

As in the case of the deltoideus, m. teres minor in the other two species of howler appears to be the same.

Nerve supply: A branch of the axillary nerve is given off in the quadrilateral space and reaches the muscle.

Function: A stabilizer of the scapulohumeral joint, it rotates the arm laterally. Its small size testifies to the relative unimportance of the muscle.

M. supraspinatus (fig. 25): This muscle is as large as the supraspinous fossa from which it arises. Peripheral fibers originating from the vertebral and cranial borders of the scapula are tendinous. They soon join the fleshy bundles arising from the rest of the excavation (fig. 24). The muscle receives an additional contribution of fibers whose origin is on the infraspinous fossa at the root of the spine. All these elements converge to form a robust and central tendon within the muscle asthis passes below the acromion. It crosses over the capsule of the shoulder joint to which it is bound by fibrous strands. The tendon inserts on the upper facet of the greater humeral tuberosity (fig. 27). A large subacromial bursa separates the supraspinatus from the acromion, coracoid, coracoacromial ligament, and distal part of the clavicle. As it traverses the joint, the tendon of the muscle covers the posterior border of the coracohumeral ligament. The supraspinatus is not different in the other howlers.

Nerve supply: The suprascapular nerve (fig. 26).

Function: It is believed that this muscle, which in man initiates the abduction of the arm, actually begins its protraction in the howler because of the angle at which the humerus is set on the scapula and the position of this last bone with respect to the thorax. This results in the eventual elevation of the arm. Otherwise, the supraspinatus stabilizes the joint.

M. infraspinatus (fig. 25): The infraspinatus is also noticeable for its strong development. It exceeds the supraspinatus in size for about one-quarter and, like that muscle, it is also of triangular shape in correspondence with the infraspinous fossa from which it originates. The surface of this spacious area is not entirely occupied by the muscle, a part near the axillary border being reserved for the two mm. teres. The fleshy fibers of the infraspinatus arise from the rest of the fossa including the under surface of the spine (fig. 24), and also from part of the infraspinal fascia. Tendinous fascicles are superficial and peripherally distributed as they come from the lower lip of the posterior border of the spine, the vertebral margin, and the proximities of the lower angle. The infraspinatus is a multipennate muscle formed by about five closely arranged bundles, all of which are directed toward the shoulder. Three of them are central with respect to the fossa, while the other two follow its axillary margin and the root of the spine. These two meet superficial to the other three near the neck of the scapula. At this level a central and powerful tendon is formed which crosses the back of the scapulohumeral capsule, adheres to it, and is inserted on the intermediate

facet of the greater tuberosity (fig. 27). The muscle is apparently the same in the other howlers.

Nerve supply: The suprascapular nerve.

Function: It is another stabilizer of the joint and is an abductor and lateral rotator of the arm.

Comparative anatomy of the intrinsic series.—In none of the animals with which I am comparing *Alouatta* does there appear to be any significant deviation from the patterns here described for the muscles of the intrinsic series. Information about them was obtained from Ashton and Oxnard (1963), Campbell (1937), Hill (1962), and Senft (1907) for *Ateles;* Hill (1962) for *Brachyteles;* Campbell (1937), Hill (1962), and Robertson (1944) for *Lagothrix;* Campbell (1937), and Senft (1907) for *Cebus.* A comment should be added. Ashton and Oxnard (1963) explain that the area of the angle taken up by the origin of the muscle teres major is larger in quadrupeds than in semibrachiators. I observed it to be large in *Alouatta* (fig. 24).

Upper Arm Group

M. triceps brachii (fig. 28): The strong and large triceps is formed by three well-developed portions. The caput longum arises from the upper half of the axillary border of the scapula (fig. 24) and from the infraspinal fascia that surrounds both teres minor and the infraspinatus. Its origin is thereby extended across the surface of these two muscles to the spina scapulae. Lateral fibers of this head are tendinous and come from as high up as the attachment of the articular capsule on the scapula. The medial fibers are muscular. The long head runs distally covered by m. dorso-epitrochlearis. At about the middle of the arm or above, it joins the lateral head to form a single muscular mass which occupies the entire dorsum of the arm and covers the medial head. In one powerfully built male its components were differentiated into two more or less independent parts. Fleshy superficial fibers came from the border of the bone and adjacent infraspinal fascia to form a voluminous bundle directed distally. Tendinous and deep fibers with origin near the glenoid labrum had a spiral-like course around the superficial fibers. Both portions joined with the lateral head. The caput laterale arises from the upper half of the lateral border of the humerus where its attachment contributes to form a well-marked deltotricipital crest. Its fibers of origin are a mixture of short tendinous and fleshy elements, some of which expand a bit into the posterior surface of the bone. They reach the surgical neck. This head is directed distally until it meets the long one. As the combined belly approaches the elbow, it forms a broad tendon by means of which insertion is made

on the dorsum and tip of the olecranon. The caput mediale is formed by fibers arising from the entire dorsal surface of the humeral shaft, except where this area is occupied by the origin of the lateral head. The caput mediale is a separate muscular mass which runs under cover of the other two. Its insertion is on the tip of the olecranon

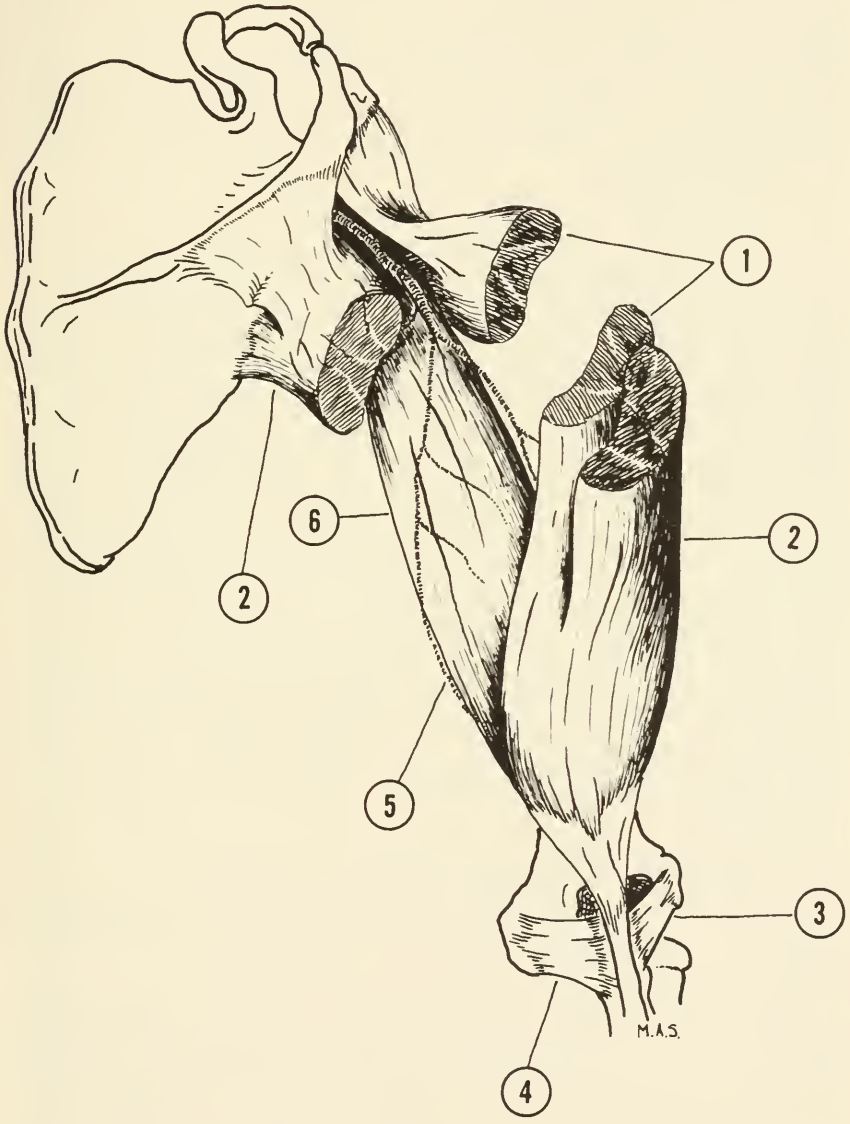

FIGURE 28.—Dorsal view of the arm and shoulder (1, m. triceps brachii, caput laterale; 2, m. triceps branchii, caput longum; 3, m. anconeus; 4, m. epitrochleo-anconeus; 5, n. ulnaris collateralis; 6, m. triceps brachii, caput mediale.

and the deep surface of the tendon formed by the other two heads.

The muscle is not different in the howlers studied by other authors (Campbell, 1937; Sirena, 1871; Ashton and Oxnard, 1963).

Nerve supply: The long head receives a high branch of the radial nerve. In one male, the lower branch of the axillary nerve sends an additional twig to it. The medial head is innervated by several branches of the ulnar collateral nerve; the lateral by the radial, as this spirals around the humeral shaft.

Function: Its strong development indicates the importance of the muscle as extensor of the antebrachium. In addition, the broad scapular attachment allows the triceps to retract the arm at the scapulohumeral joint.

M. dorso-epitrochlearis: This is a broad but flat muscular band found superficially on the dorsomedial aspect of the arm immediately beneath the skin and brachial fascia. It arises by fleshy fibers from the lower border and adjacent parts of the anterior and posterior aspects of the latissimus tendon, as this travels through the floor of the axilla. The dorso-epitrochlear fibers run distally, covering the triceps and narrowing down to about one-half of the original width of the muscle as they approach the elbow. The fleshy fascicles now become continuous with the fibrous tracts of the brachial fascia. In this manner the dorso-epitrochlearis gains insertion to the medial epicondyle, its ridge, and the olecranon. There is some grouping of fibers in the part of the fascia leading from the distal end of the muscle to the dorsum and medial aspect of the olecranon, but this was not always a very obvious detail.

Sirena (1871) describes a similar muscle, but only the olecranal ending. Ashton and Oxnard (1963), on the other hand, assign the insertion to the medial epicondyle. Campbell (1937) adds that the muscle has its origin extended to the axillary border of the scapula by means of a condensation of fibrous tissue within the substance of the latissimus.

Nerve supply: The first branch given off the radial nerve, before entering the radial canal, is for the dorso-epitrochlearis.

Function: It has a combined action of extensor of the forearm through its fascial continuation to the olecranon, and adductor of the arm.

Comparative anatomy of the upper arm group.—The triceps brachii appears to be the same in the other genera. *Alouatta* also shares with them the supplementary anchorage of the long head to the spine of the scapula by means of the infraspinal fascia (Campbell, 1937; Hill, 1962). The distal attachment of m. dorso-epitrochlearis is variously described by those who have studied the muscle. In *Ateles* it is reported to end on the intermuscular septum and epicondyle by

Ashton and Oxnard (1963). Schück (1913a) indicates that in most of his specimens of *Cebus* and *Ateles* the muscle ends on the intermuscular septum and he observed a thickening of the brachial fascia following the direction of the fleshy fascicles. The termination of these fibrous strands is, however, not stated. According to Hill (1962), the dorso-epitrochlearis merges with the intermuscular septum above the epicondyle in the woolly spider monkey. In *Lagothrix* (Robertson, 1944) it appears to have the same arrangement I have described for the howler. It is evident that in all these five platyrrhines the muscle ends above the elbow in the fascia of the arm, which acts as an intermediary structure between the fleshy bundles and its own attachment to the medial epicondyle, the ridge, and the olecranon.

Forearm Group

SUPERFICIAL SERIES, RADIAL DIVISION

M. brachioradialis: Its long and transversely flattened belly is found along the preaxial margin of the forearm. Origin is by fleshy fascicles from the lower third of the lateral margin of the humerus and most of the supracondylar ridge (fig. 27). The medial aspect of the muscle is here strongly connected to the sheaths of m. biceps and the brachialis. The fibrous strands are organized as lamellae. The brachioradialis runs distally covering the two radial extensors of the carpus. Some of the superficial fibers of the muscle leave its posterior border to reach the intermediate third of the radius by following the lateral intermuscular septum. Brachioradialis becomes gradually narrower until at the distal fifth of the antebrachium its fibers end on a flat tendon that has formed in the deep aspect of the muscle. This structure is firmly attached to the styloid process of the radius (fig. 27). The superficial aspect of brachioradialis is related to the skin and to the branches of the posterior cutaneous nerve of the forearm. The cephalic vein runs proximally over its anterior border. The radial and musculocutaneous nerves enter the forearm after running between m. brachialis and the three humeroradial muscles together with the radial recurrent artery. The radial artery now joins the nerve on whose medial side it runs along the deep aspect of the brachioradialis as far as the lower third of the antebrachium. They pass dorsally between the tendons of the two carpal extensors and that of brachioradialis to reach the dorsum of the forearm for their distribution to the hand. The lateral antebrachial cutaneous nerve runs parallel and partially hidden by the ventral border of the brachioradialis.

Sirena (1871) regards the *supinator longus* (M. brachioradialis) of *Alouatta* as in perfect harmony with that of man. He therefore does not take into account the rather high humeral origin of the muscle in the howler.

Nerve supply: The radial nerve gives off three branches as it travels between the other humeroradial muscles and brachialis. The highest goes to brachioradialis, the intermediate to the extensor carpi radialis longus and the lowest to the brevis.

Function: Forearm flexor.

M. extensor carpi radialis longus: This is also a long and transversely flattened muscle. It connects the distal end of the humerus to the hand, is fleshy on its upper half and tendinous on the lower. The origin is by muscular fibers from the lower half of the lateral supracondylar ridge, between those of brachioradialis above and the extensor brevis below (fig. 27). The fascicles of the longus run distalward covered by brachioradialis and over those of the extensor brevis. The belly narrows down to a flat and long tendon in the middle of the forearm. This is crossed superficially by the abductor pollicis longus in the distal third of the radius. Then, it enters the second compartment of the extensor retinaculum together with the extensor brevis. The tendon now advances on the dorsolateral aspect of the carpus below those of the extensores pollicis et indices until it reaches the dorsum of the second metacarpal base where it is inserted on the radial half (fig. 29). Sirena (1871) found this muscle to be just as in man.

Nerve supply: It has already been described with the brachioradialis.

Function: Extends both carpus and metacarpus.

M. extensor carpi radialis brevis: Of a similar appearance but better developed than the other radial carpal extensor, the brevis arises by fleshy fibers from the lowest part of the lateral supracondylar ridge and the epicondyle itself (fig. 27). It runs distally toward the metacarpus, being fleshy in its proximal half and tendinous in the distal. It is covered by the other two humeroradial muscles and related on its deep surface first to m. supinator and lower down to the radius. A flat tendon is formed on the lateral aspect of the muscle upon which all its fibers converge. The tendon is covered by that of the abductor pollicis longus and then reaches the second compartment in the extensor retinaculum where it is medial to the tendon of the longus. In the carpus it proceeds distally over the scaphoid, os centralis and capitate to insertion on the well-developed styloid process of the third metacarpal (fig. 29). This structure projects radially and dorsally from the dorsum of the base.

The second radial extensor of the southern howler is also said to be like that of man, but Sirena (1871) notes that its tendon is larger than that of the first extensor.

Nerve supply: It has already been described.

Function: Extensor of the carpus and metacarpus.

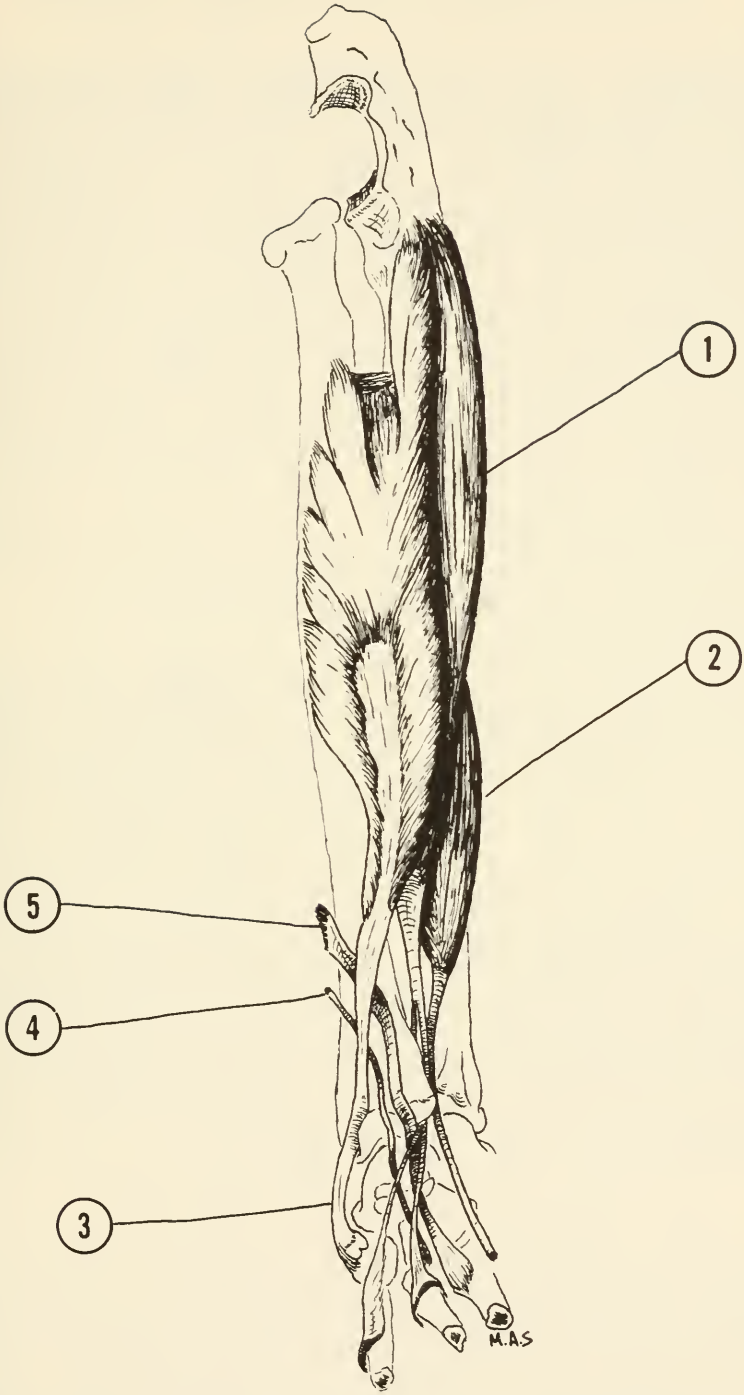

FIGURE 29.—Deep dorsal antebrachial muscles (1, m. extensor pollicis et indicis longus; 2, m. extensor digiti tertii proprius; 3, tendon of m. abductor pollicis longus; 4, m. extensor carpi radialis longus; 5, m. extensor carpi radialis brevis.

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M. supinator: This is a deeply set muscle found around the back, lateral side and front of the upper end of the radius over which it lies as a half cylinder. Supinator fascicles arise from the dorsal, lateral, and ventral aspects of the fibrous capsule of the elbow joint where they take a firm grip, particularly in the lateral ligament. The most medial of its dorsal fibers originate from a rugosity found behind the lesser sigmoid cavity in the ulna. Some of the lateral fascicles have a tendinous origin from the dorsal and lower end of the lateral epicondyle. All its bundles follow a spiral direction around the radius and they end on the lateral surface of this bone lateral to the bicipital tuberosity and between the insertions of the capsular ligaments of the joint above and the pronator teres below (fig. 27). The superficial and lateral fibers of the supinator are tendinous and form a thin cover to the dorsal interosseous nerve which penetrates the muscle on its way to the dorsal antebrachial compartment.

Once more Sirena (1871) compares the howler with man and finds no difference between the muscles of the two animals.

Nerve supply: A branch of the dorsal interosseous nerve.

Function: Supination.

Comparative anatomy of the radial division.—The brachioradialis muscles of the spider (Hill, 1962), woolly (Hill, 1962; Robertson, 1944) and woolly spider monkey (Hill, 1962) are entirely similar to that of the howler. The fibrous connection with the sheath of m. brachialis is described by Robertson (1944) as an additional origin in *Lagothrix. Cebus* (Hill, 1960; Straus, 1941) offers no difference from this pattern. The two carpal extensors also appear to be similar in all these animals (Hill, 1962; Robertson, 1944), except in *Cebus* where Straus (1941) found the brevis tendon inserted in both metacarpals II and III. Senft (1907) was not able to differentiate the two muscles proximally in *Ateles ater* (=*Ateles paniscus*). He describes them as arising by a common belly from both the humerus and the epicondyle. All the authors agree that the tendon of the extensor brevis is always more robust than that of the longus. No significant difference can be pointed out about m. supinator either. Robertson (1944) noted a large epicondylar origin for this muscle in *Lagothrix.*

SUPERFICIAL SERIES, INTERMEDIATE DIVISION

M. extensor digitorum: From the tip (fig. 27) and dorsum of the lateral epicondyle short tendinous fibers take origin and soon become muscular to form a flat and elongated belly which runs distally between m. extensor carpi radialis brevis laterally and the fifth digital extensor medially. Many fascicles of the extensor digitorum arise from the aponeurotic septa between it and the other two muscles. At the distal third of the forearm the belly transforms into five round,

narrow, and long tendons which pass into the hand through the third, from radial to ulnar, compartment of the extensor retinaculum. It is here accompanied below by the tendons of the deep extensor muscles. This narrow and deep compartment is formed at each side by the nonarticular portions of the adjacent and distal ends of the two antebrachial bones. The tendons of the extensor digitorum, which can be numbered 1 to 5 from the radial to ulnar side, reach the dorsum of the carpus under cover of the local blood vessels and nerves. Here they are united by connexus intertendineus into a triangular lamina at the distal or basal end of which four flattened bands extend toward digits II to V. Those to II and V are smaller. Of the five original tendons, number 1 contributed its fibers to digits II and III, number 2 to III, 3 to III and IV, 4 to IV and V, 5 to V. The common triangular lamina is tightly contained within a subdivision of the superficial layer of the deep manual fascia. The arrangement of every one of the tendinous bands to the digits is similar. Each runs distally over the two proximal phalanges of the corresponding finger and is inserted at the base of the distal phalanx on its dorsal aspect. It is closely bound to the capsule of the first interphalangeal joint, and after crossing the metacarpophalangeal articulation, it sends toward the palmar aspect of the hand a pair of expansions, one at each side. These are connected to the capsular ligaments and receive distally the insertions of the interossei and lumbrical muscles.

The observations in *Alouatta fusca* (Sirena, 1871) are like mine except that the tendons are said to end as in man.

Nerve supply: The dorsal interosseous nerve supplies several branches to the deep aspect of the muscle.

Function: Extensor of the distal phalanges of digits II to V.

Comparative anatomy: The extensor digitorum is equal in *Alouatta*, *Ateles* (Senft, 1907; Hill, 1962), *Brachyteles* (Hill, 1962), *Cebus* (Senft, 1907; Straus, 1941) and *Lagothrix* (Robertson, 1944). The distribution of the five original tendons of the muscle in the last genus resembles very closely the one I described for the howler, except that the fifth tendon in the woolly monkey contributes to both IV and V digits. Information in this respect was not available about the other animals. Robertson (1944) includes the belly of an extensor digiti minimi with that of the extensor digitorum in his description of the latter.

SUPERFICIAL SERIES, ULNAR DIVISION

M. anconeus (fig. 28): It was present on both sides of only one of my specimens and could be seen as a triangular muscle with the apex at the dorsum of the lateral epicondyle and the base on the radial border of the olecranon. The upper fibers were not easily differentiated from those of the triceps, but the lower ones formed a

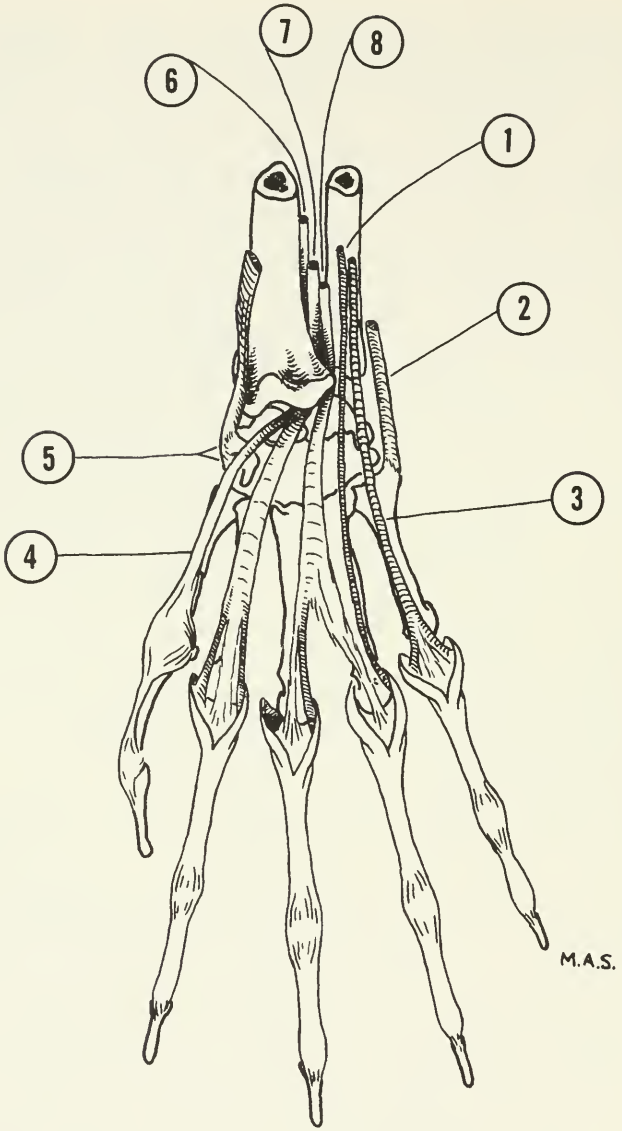


FIGURE 30.—Dorsal view of the left hand (1, smaller tendon of m. extensor digiti quinti et quarti proprius; 2, tendon of m. extensor carpi ulnaris reaching the styloid process of metacarpale V; 3, large tendon of m. extensor digiti quinti et quarti proprius; 4, tendon to digit I of m. extensor pollicis et indicis longus; 5, tendon of m. abductor pollicis longus reaching the radial carpal sesamoid and trapezius; 6, as no 4; 7, tendon to digit II of m. extensor pollicis et indicis longus; 8, tendon of m. extensor digiti tertii proprius).

clear border delimiting anconeus from the extensor carpi ulnaris. It is said to be like that of man in the southern howler (Sirena, 1871).

Nerve supply: The radial nerve.

Function: Sirena (1871) attributes to it a function similar to that of the epitrochleo-anconeus.

M. extensor carpi ulnaris: This is the most medial of the dorsal and superficial antebrachial muscles. It arises by tendinous and fleshy fibers from the lower border and back of the lateral epicondyle. It forms an elongated and flat muscular belly, passing distally superficial to the supinator and the shaft of the ulna. A tendon develops on its medial border upon which the fibers of the muscle are inserted as far down as the lower third of the forearm. As it approaches the carpus, the tendon of the extensor carpi ulnaris passes through the ulnarmost of the extensor retinacular compartments and glides on a groove of the distal end of the ulna. In the dorsum of the hand it is covered by the other extensor tendons and finally is inserted on the ulnopalmar half of the styloid process in metacarpale V (fig. 30). The ending of the muscle is also on the ulnar side of metacarpale V of *Alouatta fusca* (Sirena, 1871).

Nerve supply: The dorsal interosseous nerve innervates the muscle by a branch to the deep aspect of its proximal fourth.

Function: Abducts and dorsiflexes the metacarpus and carpus on the forearm.

M. extensor digiti quinti et quarti proprius (=extensor digiti minimi of N.A.): This is also a superficial muscle of the dorsum of the forearm found between the extensor digitorum laterally and the extensor carpi ulnaris medially. Origin is by short tendinous fibers from the lower end of the lateral epicondyle (fig. 27) and from the aponeurotic sheath that surrounds the muscle. A belly is rapidly formed which runs distally between the extensor digitorum and extensor carpi ulnaris. Its breadth is reduced progressively until a tendon is formed in the middle of the antebrachium and which soon splits into a radial and an ulnar subdivision just before entering the fourth compartment of the extensor retinaculum (fig. 30). That of the radial side is the thinner; it reaches the fourth intermetacarpal space under cover of the carpal lamina of the extensor digitorum and is inserted on the deep aspect of the dorsal extensor expansion at the ulnar side of the fourth metacarpophalangeal joint. The ulnar tendon is stronger and flat. At the level of the fifth metacarpophalangeal articulation it broadens and is inserted on the deep aspect of each of the dorsal expansions and on the dorsal base of the proximal phalanx. According to Sirena (1871) it corresponds to the same muscle in man.

Nerve supply: The posterior interosseous nerve.

Function: Extends the fifth metacarpophalangeal joint and helps to extend and abduct the fourth.

Comparative anatomy of the ulnar division.—Senft (1907) mentions the presence of an anconeus in *Cebus*, but does not explain whether or not it was found in *Ateles*. Hill (1962) says it is absent in the spider monkey and Robertson (1944) reports it in *Lagothrix*. When discussing the musculature of the cebids in general, Hill (1960) claims that the muscle is arranged exactly as in man. I suspect that there might be individual variability.

The ending of m. extensor carpi ulnaris is on the medial side of the fifth metacarpal base in *Ateles* (Senft, 1907) and *Brachyteles* (Hill, 1962), on its volar surface in *Lagothrix* (Robertson, 1944) and *Cebus* (Senft, 1907; Straus, 1941). In all these animals, as well as the howling monkey, the muscle is probably more an abductor of the carpus than an extensor.

Only *Brachyteles* (Hill, 1962) seems to have the two tendons of the extensor digiti (quarti et) quinti proprius ending exclusively on the fifth digit, one inserting on the expansion of the extensor digitorum, the other on the base of metacarpale V.

DEEP SERIES

M. abductor pollicis longus (fig. 29): This is the more laterally located of all the deep and dorsal antebrachial muscles. It has extensive origins from the radius, interosseous membrane, and ulna. Fleshy fibers spring from (1) the dorsomedial upper three-fourths of the radial diaphysis below the insertion of m. supinator, (2) the entire dorsal aspect of the upper three-fourths of the interosseous membrane, and, finally, (3) from a corresponding stretch of the ulnar shaft right behind the attachment of said membrane. The radial origin is marked by a rugosity in line with the interosseous crest. Ulnar fibers ascend up to the lateral side of the olecranon behind the sigmoid notch where a well-marked depression is found between its margin and the lateral border of the olecranon. All fibers of the abductor longus are oriented toward the radial side of the arm. A central, broad, and superficial tendon is formed very high up and receives the fascicles of the muscle. It goes around the distal end of the radius under partial cover of the brachioradialis, but itself lies over the tendons of the two radial carpal extensors. The long abductor enters the more radial compartment of the extensor retinaculum along a deep groove in the distal end of the radius. After crossing the lateral aspect of the carpus, it is inserted on both the trapezium and the radial sesamoid, which is wedged between the scaphoid and the trapezium (fig. 30). In three out of four specimens (two males, one female), three-quarters of the tendinous fibers are fixed to the trapezium,

the rest to the sesamoid. In one male they were equally distributed to the two bones, but never did I see them reaching metacarpale I.

Sirena (1871) observed the tendon of the muscle inserted by two-thirds of its fibers on the trapezium and the rest on the radial side of the first metacarpal. He also pointed out the great development of the tendon with respect to man. Grand (1967) has found in *Alouatta caraya* the same ending I have described for *Alouatta seniculus.*

Nerve supply: The dorsal interosseous nerve sends a branch to the muscle.

Function: Abductor of the carpus and hence of the whole hand.

Comparative anatomy: Hill (1962) indicates the presence in *Ateles* of an abductor pollicis longus and an extensor pollicis brevis. They are said to be well developed and their tendons, after crossing those of the carpal extensors, are inserted on the base of the first and rudimentary metacarpal. Senft (1907) regards a single belly in his specimen of *Ateles ater* (=*Ateles paniscus*) as representing the two muscles. It has origin from the radius, interosseous membrane, and ulna; insertion on the palmar side of metacarpale I. Straus (1941) studied one *Ateles geoffroyi* (=*Ateles geoffroy*) and found the abductor pollicis longus arising from the ulna and radius. Insertion was on the first metacarpal. The same muscle of *Brachyteles* (Hill, 1962) arises from both antebrachial bones to end on the trapezium and trapezoid. The double origin occurs also in *Lagothrix* where Robertson (1944) calls it *abductor carpi radialis* because of its ending on the trapezium and trapezoid bones. The abductor pollicis longus of *Cebus* comes from the ulna and radius, ending on the trapezium and metacarpale I (Straus, 1941). Senft (1907) states that in the capuchin monkey the fibers arising from the ulna correspond to m. extensor pollicis brevis and those from the interosseal membrane to the abductor pollicis longus of man, even if there is only one belly. According to him, the insertion is restricted to the first metacarpal.

The type of insertion that Grand (1967) and I have found in *Alouatta,* exclusively on the carpus (trapezium and radial sesamoid), Robertson (1944) in the woolly monkey, and Hill (1962) in *Brachyteles* (trapezium and trapezoid) corresponds to the type I of Straus (1941).

M. extensor digitorum profundus: This primitively single muscular layer is here divided into two muscles, the extensor digiti tertii proprius and the extensor pollicis et indicis longus. Both of them have only ulnar origins and are inserted into the corresponding digits.

M. extensor digiti tertii proprius (fig. 29) is the smaller and more distal of the two deep extensors. It springs from the lateral margin of the ulna along its distal half by fleshy fibers directed laterally and distally toward the axis of the forearm. It is covered by both the extensor

carpi ulnaris and the extensor digiti minimi. A small and round tendon is formed when the muscle enters the central compartment of the extensor retinaculum, where it lies deep to the tendons of the extensor digitorum and on the medial side of those of the extensor pollicis et indicis longus. In the hand, the tendon is deep to the central carpal lamina of the extensor digitorum with which it is ensheathed within the same cover derived from the superficial layer of the deep manual fascia. It finally reaches the ulnar side of metacarpale III at the metacarpophalangeal joint to end on the deep aspect of the extensor expansion. This tendon contributes a thin and fibrous band to the dorsum of the first phalanx of the third digit, and in the left side of one male (fig. 30) a broader but thin fibrous band is supplied to the dorsum of the first phalanx of digit IV.

M. extensor pollicis et indicis longus (fig. 29) takes origin by fleshy fibers from the upper half of the lateral border of the ulna, above the origin of the extensor tertii. Its fibers come from as high up as the junction with the lateral border of the olecranon. They pass distally toward the axis of the limb covered by the extensor carpi ulnaris and the extensor digiti minimi. Before entering the central and main compartment of the extensor retinaculum a short tendon is formed which rapidly splits into two, one for the second digit and the other for the first. In the carpus and metacarpus they are both apposed to the deep aspect of the central carpal lamina of the extensor digitorum with which they are contained in the subdivision of the superficial layer of the deep manual fascia. The tendon for the second digit provides three expansions (fig. 30); a tendinous one goes to the ulnar side of the second metacarpophalangeal joint where it ends on the deep aspect of the dorsal extensor expansion on that side; a second weak and membranous band goes to the dorsum of the base of the first corresponding phalanx, while the third is similar to the first and joins the radial extensor expansion on its deep aspect. The tendon for the first digit ends dorsally on the base of the last pollical phalanx. It gives off membranous expansions at each side of the first metacarpophalangeal joint. These pass ventrally along the capsular ligaments to which they are connected. Obliquely running fibrous fascicles pass from one tendon of the muscle to the other over the carpus.

In talking about the representatives of the extensor digitorum profundus in *Alouatta fusca*, Sirena (1871) calls the extensor pollicis et indicis longus, m. extensor pollicis longus, but his description practically matches mine in origin and insertions. The same is the case with the extensor digiti tertii proprius which he calls m. extensor indicis proprius, borrowing from the terminology of human anatomy.

Nerve supply: Both components of the extensor profundus are innervated by branches of the dorsal interosseous nerve.

Function: The extensor of the index and pollex extends the first digit at both the metacarpophalangeal and interphalangeal joints, but only the metacarpophalangeal articulation of the second. M. extensor tertii proprius produces a similar effect upon the third digit at the metacarpophalangeal level and by its ending on the ulnar side expansion of the extensor digitorum tendon, it abducts this finger. This attachment of the extensor of the third digit and that of the smaller tendon of m. extensor digiti minimi to the same side on the fourth and third finger is, perhaps, one of the anatomical bases for the zygodactylous grasp in *Alouatta*. Conceivably, the other might be the control of the pollex and index by one single muscle, the extensor pollicis et indicis longus.

Comparative anatomy: The division of the deep digital extensor of the forelimb into a first part for the index and pollex and a second for the other digits appears to be found normally only in platyrrhines and *Tarsius* (Straus, 1941). My observations in *Alouatta seniculus* and those of Sirena (1871) in *Alouatta fusca* sustain this generalization, but the situation is not so clear in *Ateles*, *Brachyteles*, *Lagothrix*, and *Cebus*. The description of this muscle, or its parts, is not always done with the same approach and the results of the wording are sometimes confusing. The arrangement described for *Lagothrix* by Robertson (1944) appears to resemble that of the howler in the existence of two separate tendons for digits I and II coming from a single muscular belly, but it seems as if, in this genus, contributions are given also to III and IV before the subdivisions to the pollex and index had formed. In *Brachyteles* (Hill, 1962) the deep extensor is said to be represented by two bellies which, after origin from the radius, form fine tendons destined to join the dorsal expansions of the index. The pattern reported by Senft (1907) in *Ateles* is that of a deep extensor dividing into three parts, one joining the extensor aponeurosis to III, the other two blending with that to II. What he describes as m. extensor pollicis longus in *Cebus* with origin from the middle third of the ulna and interosseous membrane divides into tendons, one for the first digit, the other for the second and third. Straus (1941) reports a separate extensor pollicis longus in one *Cebus*. It seems as if these ceboids are no exception to the great variability which the second part of the deep extensor has been shown to have in all primates (Straus, 1941).

Ventral (Flexor) Musculature

Shoulder Girdle Group

EXTRINSIC SERIES

M. pectoralis major: This triangular muscle narrows from its extensive origin along part of the clavicle and the midline of the

thorax towards its insertion on the upper part of the humeral diaphysis (fig. 31). Sternoclavicular and sternocostalis parts can be recognized but not separated. The first arises by thick, fleshy bundles from the ventral aspect of the medial clavicular half, the capsule of the sternoclavicular joint, the sternal process, and the remainder of the manubrium. Pars sternocostalis has a muscular origin from the lateral half of the sternum, adjacent sternocostal joints and cartilages down to the sixth in all the males, but only to the fourth in the female. The caudal part of the pectoralis major in front of the sixth cartilage actually comes from the rectus sheath. The sternoclavicular fibers run horizontally outward, while the sternocostals follow an increasingly oblique and ascending direction toward the shoulder. The insertion is on the upper two-thirds of the crest of the greater tubercle (fig. 27) by a double layered, strong, and flat tendon. Its two laminae are joined along their caudal margins and formed as follows: (1) the superficial by the sternoclavicular fibers, (2) the deep by those with sternocostal origin. The distal portion of the pectoralis major is partially covered near its insertion by the pars clavicularis of m. deltoideus, the two muscles being intimately connected by fibrous tissue with the cephalic vein running along the deltopectoral interval. This same part of the pectoral lies over the two heads of the biceps, m. coracobrachialis, and the latissimus tendon. More medially, the pectoralis major contributes to form the ventral axillary wall and, over the thorax, it covers the other two pectorals.

Sirena (1871) considers this muscle in *Alouatta fusca* to be in general like that of man but contrasting in (1) the lack of separation between pars clavicularis and the sternocostalis, and (2) the midline intercrossing in front of the sternum. A clavicular origin occurs also in *Alouatta palliata* (Campbell, 1937). Hill (1962) states that the clavicular origin takes place on the medial sixth of that bone and that the sternocostal origin covers the first six ribs.

Nerve supply: The lateral pectoral nerve from C VI and VII (fig. 26).

M. pectoralis minor (fig. 31): This is an elongated and flat muscle found close to the midline of the rib cage deep to the pectoralis major. Its origin lies between the sternum and the highest costal digitations of m. rectus abdominis. It begins by fleshy fibers from the ventral aspect of the third, fourth, and fifth costal cartilages, but from the first to the third in the female. The fascicles form broad digitations that reach the muscle on its deep surface. Pectoralis minor ascends craniolaterally in front of the first five ribs, passes across the subclavius muscle and the clavicle to reach the shoulder as a strong and flat tendon. The insertion is on the ventromedial

border of the coracohumeral ligament. Its lateral margin is covered by the medial bundles of m. pectoralis abdominis. These two muscles are closely joined by connective tissue, but still clearly differentiated from each other. Sirena (1871) thought that they formed a single pectoralis minor, but Campbell (1937) was able to identify them separately in *Alouatta palliata*.

Nerve supply: The medial pectoral nerve with contributions from C VI and VII or VIII (fig. 26).

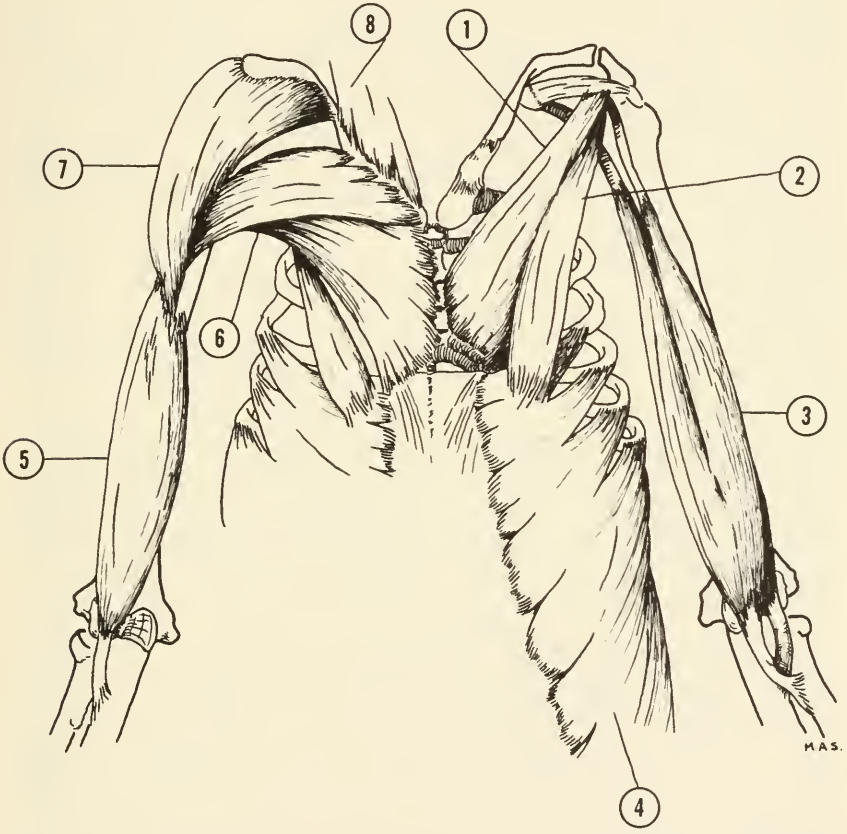


FIGURE 31.—Ventral view of the thorax and shoulder (1, m. pectoralis minor; 2, m. pectoralis abdominalis; 3, m. biceps brachii; 4, m. obliquus externus abdominis; 5, m. brachialis; 6, m. pectoralis major; 7, m. deltoideus; 8, m. sternocleidomastoideus).

M. pectoralis abdominalis: This is also an elongated muscle broader at its costal than at its humeral end. It arises by fleshy fibers from the rectus sheath in front of approximately the sixth intercostal space and cartilage. This origin is higher in the female. The ventrally compressed belly reaches the shoulder where it changes into a progres-

sively narrower aponeurotic band. Insertion is on the ventral part of the lesser tuberosity (fig. 27).

Nerve supply: A branch from the ansa pectoralis.

M. subclavius: A strong and elongated muscle found between the scapula and the lower surface of the clavicle at one end, and the first rib at the other. It has an approximately oval cross section which is larger near the shoulder than at the thorax. The muscle arises by fleshy fibers from the upper surface and distal end of the first rib where some of them come also from the corresponding costochondral joint. Its belly is directed laterally, cranially and a little backward, crossing the costoclavicular space to reach the region of the coracoclavicular joint. The subclavian bundles are inserted on the posteromedial surface of the trapezoid ligament (the conoid is absent) and adjacent inferior surface of the clavicle. A sharp edge is usually formed in the posterior border of the bone at the attachment of the muscle (fig. 24). A large insertion occurs also on the base of the coracoid process which is flattened and expanded for the reception of the subclavian bundles. Finally, some of its fibers reach the suprascapular ligament and the lateral border of the notch (fig. 24). The muscle is surrounded by the clavipectoral fascia. The coracoid insertion is also indicated by Ashton and Oxnard (1963), Campbell (1937), and Sirena (1871).

Nerve supply: A branch from the brachial plexus (see fig. 26).

Function of the extrinsic muscles.—The pectoral mass acts in medially rotating the proximal segment of the forelimb (pars sternoclavicularis). It is also important in pulling back the segment as in retracting the arm (pars sternocostalis). The subclavius is a stabilizer of the pectoral girdle.

Comparative anatomy of the extrinsic series.—The clavicular origin of m. pectoralis major occurs also in *Lagothrix* (Ashton and Oxnard, 1963; Campbell, 1937; Hill, 1962; Robertson, 1944), in *Brachyteles* (Hill, 1962) where it is said to be reduced to a small slip, and in *Ateles* (Ashton and Oxnard, 1963; Hill, 1962). Campbell (1937) negates its presence in the spider monkey and Hill (1962) comments that it is often thin and aponeurotic in this animal. The howling monkey conforms with the semibrachiators of Ashton and Oxnard (1963) in (1) the more prominent development of the sternoclavicular part of the muscle and (2) the extent of the muscular origin on the thorax. In quadrupeds the pars sternocostalis is the stronger and reaches the eighth rib in 78.5% of their cases (Ashton and Oxnard, 1963).

There are again no differences among *Ateles, Brachyteles, Lagothrix,* and the howling monkey in the other two pectoral muscles and the subclavius. *Cebus,* on the other hand, lacks a pars clavicularis

(Campbell, 1937; Hill, 1960) and the minor arises only from the sternum (Campbell, 1937; Hill, 1960).

INTRINSIC SERIES

Of the two muscles included here by Straus (unpublished), only the coracobrachialis will be studied under this heading. The biceps brachii, caput breve is considered with the next group because of topographic and functional reasons.

M. coracobrachialis: The muscle is divided into two parts and extends from the short bicipital head to the humerus. (1) Pars profunda is formed by fleshy fibers which split off the deep surface of the caput breve tendon very near the coracoid process. Its short belly is directed toward the surgical neck of the humerus where its ending shows some variability. In two males, after passing in front of the subscapular tendon, the pars profunda turns backward around its caudal margin, gaining a fleshy attachment to the surgical neck between the buttresses of the head and lesser tuberosity. In another male and in the female the insertion occurs on the lesser tuberosity between the attachments of m. pectoralis abdominalis in front and the powerful subscapular tendon behind (fig. 27). In the first case the coracobrachialis ending projects a little into the origin of m. vastus lateralis, in the second its more distal fibers are covered by the highest ones of the latissimus. (2) Pars media arises also by fleshy fibers from the deep aspect of the short tendon, a little beyond the origin of the profunda fibers. Its fusiform belly follows the same direction as the caput breve bicipitalis, passes in front of the latissimus tendon and has a fleshy ending just distal to and a bit in front of the attachment of that tendon (fig. 27). I found the musculocutaneous nerve invariably passing between the two parts of the muscle.

Sirena (1871) did not note the division of the muscle into partes profunda and media. Howell and Straus (1931) did not find the pars profunda in *Alouatta* but Campbell (1937) speaks of both portions as present in all the animals he studied, including one *Alouatta palliata.*

Nerve supply: The pars profunda receives one or more small branches from the musculocutaneous before this nerve passes through the two heads. The caput media is supplied by a more distal twig from the same nerve. In the illustrated diagram of the brachial plexus these nerves are shown coming directly from the lateral cord (fig. 26).

Function: Flexor of the arm.

Comparative anatomy: Howell and Straus (1931) found a slender pars profunda in *Ateles* and in only one out of two specimens of *Cebus.* Hill (1962) reports the presence of both parts in the spider monkey, but only the pars media in *Brachyteles.* Hill (1962) and Robertson

(1944) indicate that *Lagothrix* has both parts. It appears as though Senft (1907) did not find a pars profunda in either *Cebus* or *Ateles*.

Upper Arm Group

M. biceps brachii (fig. 31): It arises by two heads, a short and long, which in the ventral aspect of the arm form a pair of round and elongated muscular masses. The caput longum originates from the supraglenoid impression by a long and strong tendon which travels ventrolaterally through the capsule of the scapulohumeral joint. It then turns downward to enter the broadened and shallow bicipital groove where it is proximally covered by the transverse humeral ligament. A little beyond the surgical neck of the humerus the tendon gives rise to the muscular fibers of the lateral belly of the biceps. An equally strong tendon from the tip of the coracoid process gives rise to the caput breve. Its muscular bundles begin in front of the surgical neck of the humerus and form the medial belly. The two are closely apposed along the midline of the arm until at about the junction of the middle and distal thirds of the humerus they combine into a single and common mass. This enters the antecubital fossa between the brachialis laterally and the forearm flexors medially. It becomes now a flat and broad tendon inserted on the radial tuberosity (fig. 27). A true aponeurosis of the biceps brachii is not present, but in the antecubital fossa the muscle is connected to the mass of the forearm flexors by the antebrachial fascia reinforced by some fibrous elements.

Sirena (1871) explains that the muscle in *Alouatta fusca* is like that of man. My findings agree with those of Campbell (1937) in the Central American howler.

Nerve supply: Small branches of the musculocutaneous nerve enter each belly in the proximal part of the arm.

Function: It elevates the arm and also flexes and supinates the forearm.

M. brachialis: It is a broad muscle over the anterior aspect of the humerus (fig. 31) and covered by the biceps. The musculocutaneous nerve runs distally between these two muscles. Brachialis originates from the entire lateral and medial surfaces of the lower three-fourths of the humeral shaft (fig. 27). Its fibers ascend proximally a little higher up on the lateral side where they intervene between the insertions of m. deltoideus and the lateral intermuscular septum. The brachialis becomes laterally compressed as it approaches the elbow at the same time that it lies between the biceps and the brachioradialis. Its sheath is joined to the last muscle by abundant fibrous connective tissue. M. brachialis forms a robust tendon which, after running between that of the biceps and the capsular ligaments of the elbow, ends just distal to the coronoid process (fig. 27). Sirena (1871) offers no particular comment about this muscle in his study.

Nerve supply: The musculocutaneous nerve contributes several branches to the muscle.

Function: Flexor of the elbow.

COMPARATIVE ANATOMY OF THE UPPER ARM GROUP.—M. biceps does not have any significant variation among the five genera, with the exception of *Ateles dariensis* (=*Ateles fuscipes robustus*) where Campbell (1937) found a reduced long head with a supplementary humeral origin. The fusion of the two heads takes place far distally in the arm of *Ateles* (Howell and Straus, 1931) and *Brachyteles* (Hill, 1962). An aponeurosis biceps brachii is present in the spider monkey (Hill, 1962; Howell and Straus, 1931), *Brachyteles* (Hill, 1962) and *Lagothrix* (Robertson, 1944). It is absent in one *Cebus* dissected by Howell and Straus (1931). Senft (1907) apparently did not find it either in *Cebus* or *Ateles*. M. brachialis shows the same basic arrangement in all these five genera.

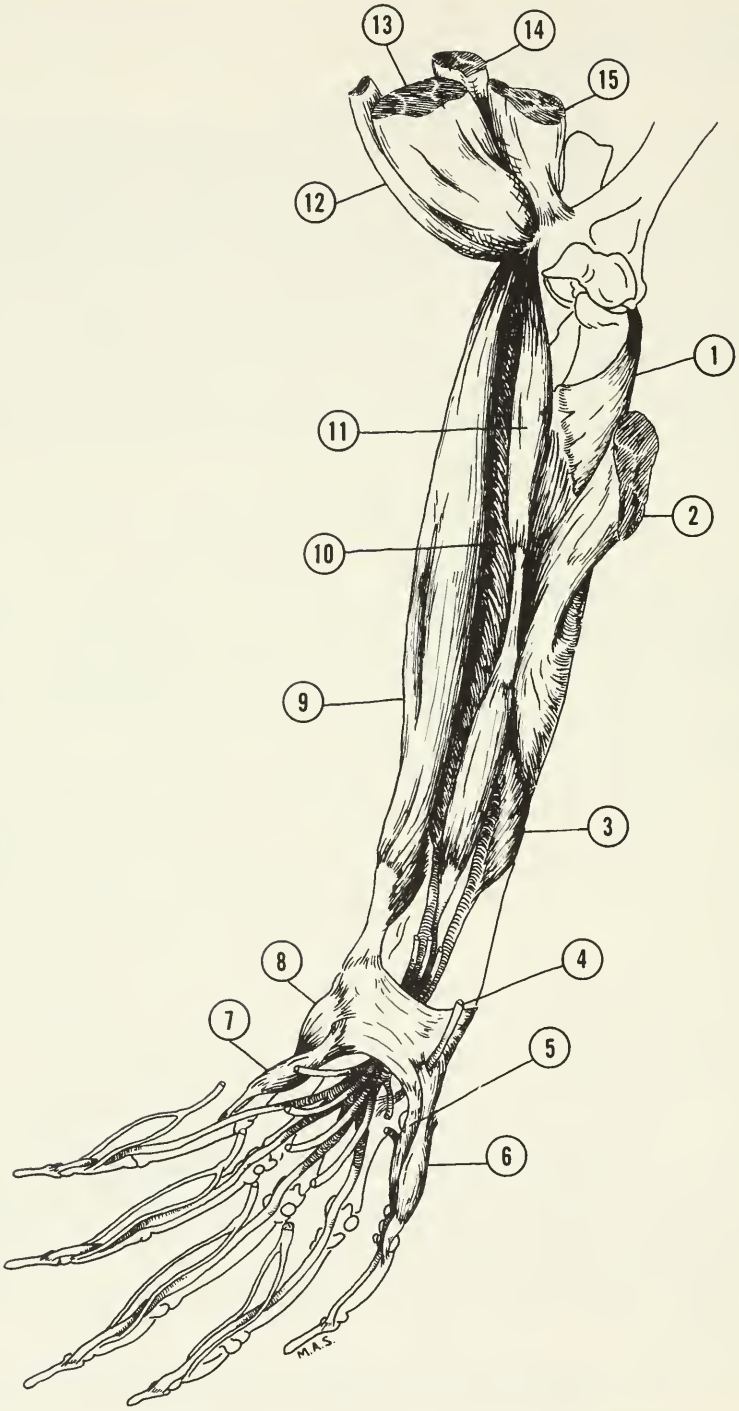
Forearm Group

SUPERFICIAL SERIES, RADIAL DIVISION

The five muscles belonging in this subdivision arise from the ventral surface of the ulnar epicondyle. Their fibers form a powerful, common fleshy mass with internal tendinous partitions separating and providing additional origins to the bundles of the different muscles. By careful dissection the precise topographical relations of their respective origins can be determined.

M. pronator teres (fig. 32): This robust and elongated muscle forms the medial boundary of the antecubital fossa. Origin is from (1) the ventral and upper part of the ulnar epicondyle, (2) the lower portion of the medial supracondylar ridge (fig. 27), (3) its own aponeurotic sheath, and (4) a tendinous septum separating the deep surface of the muscle from the superficial head of the flexores digitorum superficialis and carpi ulnaris. There is no ulnar head. The belly is oriented lateromedially, reaching the upper three-fourths of the radial shaft below the bicipital tuberosity. Insertion takes place on the ventral aspect of the bone between the origin of the radial head of the deep flexor medially and the antebrachial intermuscular septum laterally (fig. 27). This ending is formed by a mixture of tendinous and fleshy fascicles. The first forms laminae, both on the superficial and deep aspects of the muscle; the deep one in particular has continuity with the septum between the pronator and sublimis already mentioned. The rest of the insertion is all muscular. Some of the distal fibers follow the lateral intermuscular septum for some distance.

In *Alouatta fusca*, the muscle is said to be as in man (Sirena, 1871); but I wish to emphasize that it appears to be longer in the howler.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Grand's observations (1967) in *Alouatta caraya* attribute an extension of 70 percent of the radial shaft to the insertion of this muscle.

Nerve supply: It receives two branches from the medial nerve, one proximally, the other distally.

Function: I assume from the development of this muscle that pronation is an important function in the forearm of this animal.

M. flexor carpi radialis: This muscle is medial to the former and lies over the lateral border of the flexor digitorum superficialis (fig. 32). It is ventrally flattened with a proximal muscular and a distal tendinous part. It arises by mixed tendinous and fleshy fibers from the ventral and intermediate portion of the ulnar epicondyle, near fibers of the superficial head of the flexor digitorum superficialis on whose deep and tendinous side many fibers of the flexor carpi radialis take firm origin (fig. 27). The muscle runs distally across the ventral aspect of the limb toward the radial side of the carpus. It narrows down to a strong tendon on reaching the distal third of the forearm. This tendon enters a separate path in the flexor retinaculum and pierces the origin of m. abductor pollicis brevis. In the central manual compartment the tendon passes along the medial side of the trapezium crest and crosses the carpometacarpal joint of the second digit to insertion on the palmar base of metacarpale II. On the right side of one male the tendon of m. flexor carpi radialis provides a strong tendinous contribution to that of the palmaris longus.

The insertion of this muscle in *Alouatta fusca* (Sirena, 1871) and *Alouatta caraya* (Grand, 1967) is said to be on both the second and third metacarpal.

Nerve supply: The medial nerve gives off a branch which enters the muscle proximally.

Function: Flexes the hand on the forearm.

SUPERFICIAL SERIES, INTERMEDIATE DIVISION

M. flexor digitorum superficialis (fig. 32): It is found superficially in the ventral aspect of the forearm between the palmaris longus and flexor carpi radialis which conceal its medial and lateral borders, respectively. It is formed by two entirely separate parts with different origins and insertions. (1) A caput superficiale arises from the medial epicondyle between flexor carpi radialis and the pronator teres above

FIGURE 32.—Ventral view of the forearm and hand (1, m. supinator; 2, m. pronator teres, radial ending; 3, m. flexor digitorum profundus, caput radiale; 4, tendon of m. flexor carpi radialis; 5, m. flexor pollicis brevis; 6, m. abductor pollicis brevis; 7, m. flexor digiti quint (=digiti minimi of N.A.); 8, m. abductor digiti quinti (=abductor digiti minimi of N.A.); 9, m. flexor carpi ulnaris; 10, m. flexor digitorum profundus, caput ulnare; 11, m. flexor digitorum superficialis, caput profundum; 12, m. palmaris longus; 13, m. flexor digitorum superficialis, caput superficiale; 14, m. flexor carpi radialis; 15, m. pronator teres.

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and palmaris longus below (fig. 27). Fibers from this origin are fleshy superficially but tendinous where the muscle lies against the pronator teres and the flexor profundus. This head forms a ventrodorsally flattened mass which is muscular only in the proximal three-fourths of the forearm, and it gives off a slip to the radial head of the deep flexor. Distally, it changes into three round tendons for the three ulnar digits. (2) A caput profundum is totally covered by the superficialis and lies against the ventral aspect of the deep flexor. Its fleshy fibers originate also from the anterior surface of the ulnar epicondyle medially and below the caput superficiale (fig. 27). They form a narrow and long muscle which, in all specimens except one male, possesses an intermediate tendon at about the junction of the upper and middle thirds of the antebrachium. Near the wrist the distal belly forms a tendon for digit II. The four tendons of the superficialis pass below the flexor retinaculum above those of the flexor profundus. The usual arrangement is for the superficialis tendon to digits III and IV to be ventral to those to the second and fifth. In the central compartment of the hand they are between the palmar aponeurosis and the common tendinous structure of the profundus tendons and are here contained within tendomuscular tunnels formed by (1) lumbricales at each side, (2) the profundus in a deep plane, and (3) fine but resistant transverse fibrous connections between each pair of lumbricals (fig. 33a). In the digits the tendons of the superficialis travel beneath the vaginal flexor sheaths and over the corresponding tendons of the profundus. They divide at or a little beyond the metacarpophalangeal joints into two bands which thus leave an opening for the deep flexor tendon to pass through. The two bands end on the lateral margins of the second phalanx. They are joined by vincula longa to every first phalanx and by vincula brevia to every second phalanx just before they end.

Alouatta fusca has the same division of the superficial flexor (Sirena, 1871) as the red howler. The digastric deep head is called m. flexor indicis sublimis proprius by Sirena (1871) on account of its individuality. Grand (1967) has found the same pattern in howlers from northern Argentina, except that the contribution to the deep flexor comes rather from the proximal head.

Nerve supply: The median nerve provides separate branches for each head of the muscle.

Function: Flexor of the proximal interphalangeal articulation.

M. palmaris longus: This muscle lies superficially between the flexor carpi radialis and the flexor carpi ulnaris, in front of the flexor digitorum superficialis. It arises from the lowest part of the tip of the medial epicondyle, where its fibers and the epicondylar ones of the flexor carpi ulnaris are very difficult to separate (fig. 27). The

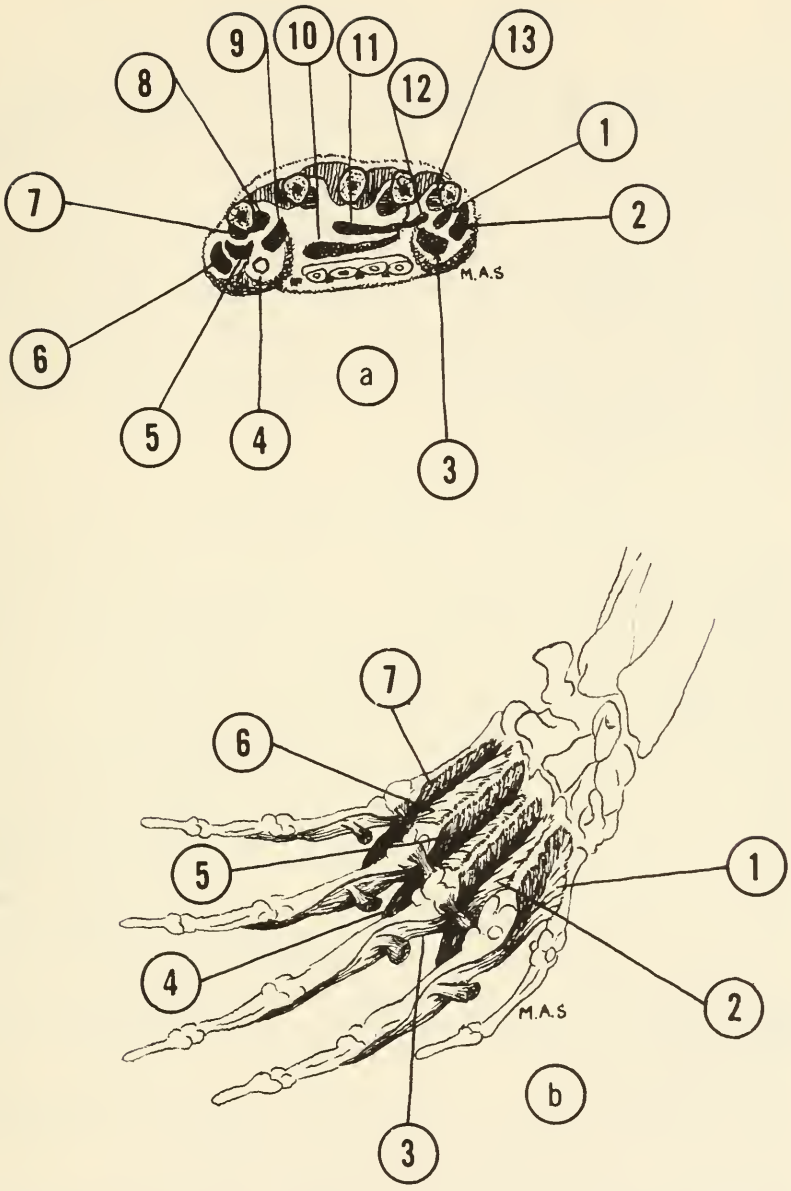

FIGURE 33.—Musculature of the hand: a, cross section (1, m. opponens digiti quinti (=opponens digiti minimi of N.A.); 2, m. abductor digiti quinti (=abductor digiti minimi of N.A.); 3, m. flexor digiti quinti (=flexor digiti minimi of N.A.); 4, tendon of m. flexor profundus to digit I; 5, m. flexor pollicis brevis, caput radiale; 6, m. abductor pollicis brevis; 7, m. opponens pollicis; 8, m. flexor pollicis brevis, caput profundum; 9 m. flexor pollicis brevis, caput ulnare; 10, m. adductor pollicis (m. contrahens I); 11, m. contrahens II; 12, m. contrahens V; 13, m. interosseus palmaris digit V) (vertical hatching=mm. interossei dorsales; horizontal hatching=mm. interossei palmares); b, mm. interossei (1, first dorsal interosseus; 2, first palmar; 3, second dorsal; 4, third dorsal; 5, second palmar; 6, fourth dorsal; 7, third palmar).

long and narrow muscular belly changes into a round tendon, thinner than that of the radial flexor of the carpus, at about the middle of the forearm. It runs along the midventral line of the limb, passes superficially to the flexor retinaculum and ends by expanding fanwise and mingling with the central part of the palmar aponeurosis.

Connections of this muscle with either of the two carpal flexors appear to be common. I found the flexor carpi radialis sending once a tendinous contribution to the palmaris longus (vide supra) and Sirena (1871) describes one case where the latter muscle received tendinous fascicles from each of the carpal flexors in the right side.

Nerve supply: A branch of the median nerve enters the muscle in the antecubital fossa.

Function: Flexes the hand.

SUPERFICIAL SERIES, ULNAR DIVISION

M. flexor carpi ulnaris: It is found medial to the palmaris longus and has a double origin. Fleshy fibers arise from the lower border of the ulnar epicondyle adjacent to those of the palmaris longus (fig. 27). They are joined by another group of similar fascicles coming from the medial border of the olecranon and ulnar shaft as far down as the distal third of the bone (fig. 27). The muscle also receives fibers arising from the medial antebrachial intermuscular septum. They all pass distally, forming a large and anteroposteriorly flattened belly on whose deep aspect we find the ulnar artery and nerve as they run toward the hand. Bundles from the distal third of the ulna are separated from the rest, forming an apparently separate head. The fibers of the flexor carpi ulnaris end on a central tendon formed inside the muscle in the distal fifth of the forearm. It is short and attaches to the proximal surface of the large pisiform. Sirena (1871) also notes the double origin of the muscle, but he does not say what length of the ulna is taken up by its fibers. Grand (1967) agrees also as to its robustness.

Nerve supply: The ulnar nerve sends a proximal branch to the upper part of the muscle, and the dorsal carpal branch supplies a smaller twig to the slip from the distal third of the ulna.

Function: A powerful flexor of the carpus.

M. epitrochleo-anconeus (fig. 28): This small and well-defined muscle was found in both sides of my four specimens. It bridges the distance between the dorsum of the ulnar epicondyle and the medial surface of the olecranon as a muscular arch underneath which the ulnar nerve passes into the forearm. Sirena (1871) also notes its presence.

Nerve supply: The ulnar nerve innervates the muscle through a short branch that also goes to the joint.

Function: According to Sirena (1871), this muscle and the anconeus are synergists in keeping the olecranon in place against the pull of the dorso-epitrochlearis.

DEEP SERIES

M. flexor digitorum profundus (fig. 32): The muscle is entirely covered by those of the superficial series and lies directly over the forearm bones and the interosseous membrane. The flexor profundus is formed by two heads, a caput ulnare and a caput radiale which remain separate until they form a common tendinous structure below the flexor retinaculum. (1) Caput radiale originates by fleshy fibers from an extensive area of the radius bound proximally by the tuberositas radii, distally by the attachment of m. pronator quadratus, laterally by that of the round pronator, and medially by the line along which the interosseous membrane is fixed to the radius (fig. 27). This head receives proximally a small fleshy bundle from the ulnar epicondyle and many fascicles from the tendinous sheet formed on the deep aspect of the flexor superficialis, caput superficiale. All its fibers end on a tendon which develops high up and forms the medial margin of the belly. It enters the flexor retinaculum on the radial side of the tendon of the ulnar head. Here they are both joined into a single tendinous structure, the radial fibers seeming to be contributed to digits I and II. (2) Caput ulnare has fleshy origin from the ulnar shaft over an area limited medially by the attachment to the bone of the medial intermuscular septum and the flexor carpi ulnaris, laterally by that of the interosseous membrane, and proximally by the brachialis insertion, although a good many of the flexor fibers ascend over the medial surface of the olecranon to the proximity of the upper end of this process. Distally the area of origin stops where the fibers of pronator quadratus are inserted on the ulna (fig. 27). The fibers of this head insert on a long tendon which develops along its radial margin and later on, in the carpal canal, it joins the tendon of the radial head. The fascicles of the ulnar head seem to go to digits III, IV, and V. From the common central structure five tendons are given off, one for every finger. That for the first is smaller and attached to the base of the distal pollical phalanx. The other four run within the fibrous flexor vaginal sheaths beneath those of the flexor superficialis, which they perforate to end on the palmar base of the last respective phalanx. Individual vincula brevia unite them to the second phalanges.

The information about this flexor in *Alouatta fusca* is obscured by the attempt of Sirena (1871) to name the parts of this muscle with terms used in human anatomy. Nevertheless, the pattern he describes corresponds to that of my red howlers.

Nerve supply: The radial head is innervated by branches of the median nerve, the ulnar by the ulnar nerve.

Function: Flexes the distal interphalangeal joints of all the fingers.

M. pronator quadratus: This is a trapezoid-like muscle found between the tendons of the flexor profundus and the distal fourth of the ulna and radius. The base of the trapezoid corresponds to the origin by intermingled fleshy and tendinous fibers from the anterior surface of the distal fourth of the ulna (fig. 27). A sharp longitudinal ridge here indicates the attachment of the pronator quadratus. Proximal bundles slope down and laterally toward their ending, whereas the more distal elements pass radially in a rather horizontal course. The muscle thus covers the interosseous membrane before having a fleshy insertion on the distal end of the radius (fig. 27). The finding of Sirena (1871) in *Alouatta fusca* calls for no special comment.

Nerve supply: The ventral interosseous nerve reaches the muscle on its deep surface to innervate it.

Function: Pronation.

Comparative anatomy of the forearm group.—M. pronator teres of *Cebus* (Laugier, 1933) appears to have a shorter radial ending than in any of the other four genera under consideration. Senft (1907), nevertheless, describes it as covering the intermediate and distal thirds of the forearm. In other details the muscle is the same in all five genera. The two carpal flexors do not offer significant differences (see Hill, 1962; Robertson, 1944; Senft, 1907). I found the flexor superficialis of an adult female *Ateles sp.* divided into superficial and deep parts. The first is a large belly quite like that of *Alouatta* in origin, topographical relations and endings. The second, on the other hand, is not fusiform or two-bellied, but a rather broad, flat mass smaller than the superficial and originating deep to it on the ulnar epicondyle and the strong aponeurotic septum together with m. flexor carpi ulnaris (Schön, 1965). The same division is reported by Hill (1962) for the spider monkey, where the pars profunda is said to have radial and ulnar halves. Senft (1907) did not describe this arrangement into superficial and deep portions in this study on *Ateles*. The findings of Robertson (1944) in the woolly monkey are comparable to ours in the howler. In his case the deep segment of the superficial flexor has both an ulnar and a medial epicondylar origin. He did not find this head divided by an intermediate tendon. The flexor superficialis of *Brachyteles* (Hill, 1962) is not so split.

M. flexor profundus of the female *Ateles* that I examined had robust ulnar, radial, and central parts, the first two with origins comparable to those in the howler, the last arising mostly from the flexor epicondyle but with some of its fibers coming from a poorly defined raphe extended between the radius and that epicondyle. Its tendon joins that of pars radialis. Hill (1962) gives a comparable account

of the muscle for this genus, but the central part is said to come only from the raphe. The description by Senft (1907) of the flexor profundus is incomplete. He does not mention the conspicuous pars ulnaris and points out that m. flexor pollicis longus is absent. The formation of a common tendon by the different parts of the muscle, in the carpal canal, is described by Hill (1962) and Senft (1907), but Straus (1949) shows one case of *Ateles* where the fusion is incomplete, and I found the same situation in my spider monkey. From either the completely or partly conjoined structure, tendons are sent off to digits II to V. Those for the first two on the preaxial side of the hand derive their fibers from the combined centroradial head and are stronger. The postaxial tendons come from the ulnar belly (Schön, 1965). A triple-headed deep flexor occurs also in *Brachyteles* (Hill, 1962), where a common tendon is not mentioned in the carpal canal. The situation in *Lagothrix* (Robertson, 1944) is similar to that of the howler with radial, ulnar, and humeral parts forming a common tendon distributed to all five digits. Senft (1907) does not mention the antebrachial double origin of the flexor profundus in *Cebus*, and the muscle is said to arise apparently only from the medial epicondyle. Straus (1949) illustrates an arrangement in the capuchin monkey similar to what Grand (1967), Sirena (1871), and this writer have found in the howler, and Robertson (1944) in *Lagothrix*. The pronator quadratus of all these animals seems to be the same. An m. epitrochleo-anconeus is present also in *Brachyteles* (Hill, 1962) and *Lagothrix* (Robertson, 1944).

Hand Group

SUPERFICIAL SERIES, SUPERFICIAL LAYER

M. abductor pollicis brevis (figs. 32, 34): The more superficial and lateral of the thenar muscles is flat and not very strong. Origin is from the lateral border of the palmar aponeurosis, skin and flexor retinaculum, the navicular, and the radial carpal sesamoid. The muscle runs distally, covering part of the flexor pollicis brevis to its insertion on the radial half of the ventral base of the first pollical phalanx. This ending is fleshy and was found to be fused with that of m. flexor pollicis brevis on one side of one male and on both of another. The terminal part of the muscle glides over the radial sesamoid of the metacarpophalangeal joint in digit I. Sirena (1871) spoke of this muscle as being just as in man. That this is not true can be seen from the previous description. The abductor pollicis brevis of the howler is underdeveloped when compared to that of man. Moreover, it is not formed by two parts, receives no contribution from the long abductor, and has no insertion on the extensor

pollicis tendon, but only on the first phalanx (see Napier, 1952; and Wood Jones, 1949).

Nerve supply: A branch is given off for both the abductor pollicis brevis and the short flexor by the median nerve just before it divides into its sensory branches to the pollex, index, and half of the middle finger.

Function: It appears to be more of a flexor than an abductor of the thumb.

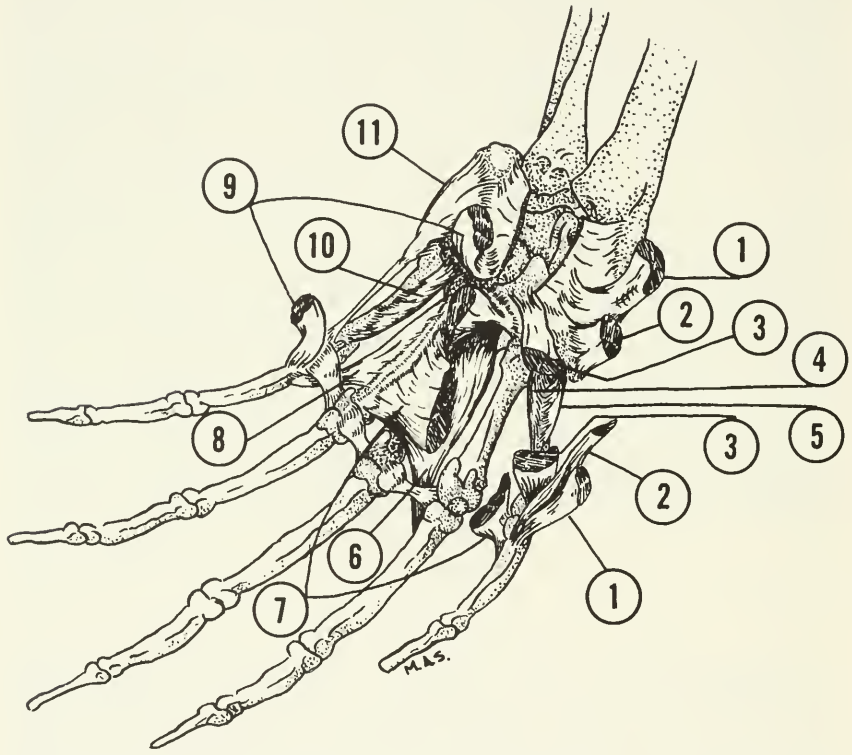

FIGURE 34.—Muscles of the hand (1, m. abductor pollicis brevis; 2, m. flexor pollicis brevis, caput radiale; 3, m. flexor pollicis brevis, caput ulnare; 4, m. flexor pollicis brevis, caput profundum; 5, m. opponens pollicis; 6, m. contrahens II; 7, m. adductor pollicis; 8, m. contrahens V; 9, m. flexor digiti quinti (=flexor digiti minimi of N.A.); 10, m. opponens digiti quinti (=opponens digiti minimi of N.A.); 11, m. abductor digiti quinti (=abductor digiti minimi of N.A.).

M. flexor pollicis brevis: This two-headed muscle is partially covered by the preceding and therefore occupies an intermediate position in depth within the thenar compartment (figs. 32, 33, 34). A caput radiale arises by strong fleshy fibers from the scaphoid and radial carpal sesamoid. The strong belly runs under that of the short ab-

ductor, decreasing in size as it approaches its end. Beyond the middle of the first metacarpal a stout and round tendon is formed and this attaches to the ventroradial base of the first phalanx. On the right side of one male and on both sides of another male this insertion is in common with that of the abductor pollicis brevis. A caput ulnare, narrower proximally but as strong as that of the radial side, arises by fleshy fibers from the fibrous sheath of the flexor carpi radialis and the trapezoid. It passes distally along the ulnar side of metacarpale I to be inserted by short and tendinous fibers on the radial tubercle of the metacarpal head. The deep flexor tendon to digit I travels between the two portions of the muscle.

Origin of the radial head in *Alouatta fusca* (Sirena, 1871) is from the flexor retinaculum and the trapezium, its insertion on the radial base of the first phalanx. The ulnar head is said to come from the trapezoid and capitate bones and to be inserted together with the rest of the muscle.

Nerve supply: The radial head is innervated by a continuation of the branch of the median to the abductor pollicis brevis. The ulnar receives a twig from the deep branch of the ulnar.

Function: By its attachment to landmarks around the metacarpophalangeal joint, but only on the radial side, these two heads can probably cause some degree of medial pollical rotation in addition to their role as flexors.

M. opponens pollicis (figs. 33, 34): It is a small but conspicuous muscle located deep to the flexor brevis and arising from (1) the palmar surface of the trapezium and (2) the flexor retinaculum. Its fibers follow a distolateral direction, cross the pollical carpometacarpal joint, and are inserted on metacarpale I for the entire proximal three-quarters of its radial shaft. Sirena (1871) claims that his howler's opponens pollicis is also just like in man.

Nerve supply: It receives a twig from the ramus of the ulnar nerve which supplies the ulnar head of the previous muscle.

Function: Its feeble development corresponds with the lack of opposability in the thumb of *Alouatta*. Indeed, the muscle probably acts only as a weak medial rotator.

M. palmaris brevis: This muscle is represented by transverse muscular fibers found in the proximal part of the hypothenar eminence, almost at the heel. They are mixed with the fatty lobules enmeshed within the fibrous strands of the subcutaneous tissue of the hand. Their origin is from the medial border of the palmar aponeurosis with insertion on the skin of the medial manual margin. Sirena (1871) describes in addition a small *m. palmaris brevis externus* on the hypothenar side.

Nerve supply: The superficial ramus of the ulnar nerve.

M. abductor digiti quinti (=*abductor digiti minimi of N.A.*): This is a well-developed muscle when compared to the small, short pollical abductor and is found on the ulnar and superficial aspect of the hypothenar eminence (figs. 32, 33, 34). It takes a firm origin on the distal surface of the ventrally projecting pisiform, while many of its superficial fibers come directly from the overlying skin. The muscle runs over the palmar aspect of the very strong pisohamate and pisometacarpal ligaments to which it is bound by the surrounding connective tissue. At the level of the carpometacarpal articulation a round tendon is formed and continues distally along the ulnar side of the fifth metacarpal, finally reaches the ulnar tubercle of the metacarpal head where it ends. The insertion, according to Sirena (1871), is on the ulnar base of the first phalanx.

Nerve supply: The superficial branch of the ulnar nerve.

Function: It abducts and flexes the fifth metacarpal.

M. flexor digiti quinti (=*flexor digiti minimi brevis of N.A.*): This is also superficial in the hypothenar side and lies along the radial margin of the abductor of the fifth digit (figs. 32, 33, 34). Strong and flat, it arises from the distal border of the flexor retinaculum. Its fibers run distomedially, covering the opponens of the fifth digit. They are inserted on the ulnar side and ulnar half of the palmar base of the proximal phalanx. Sirena (1871) considers this muscle of the howler to be just as in man.

Nerve supply: A branch of the deep ulnar nerve.

Function: A flexor of the fifth metacarpophalangeal joint. Due to its insertion on the ulnar side of the phalanx, contraction of the muscle would rotate the finger toward the axis of the hand.

SUPERFICIAL SERIES, DEEP LAYER

Mm. lumbricales: These are four long, cylindrical muscles which from their origins between the perforating tendons pass distally in the middle compartment of the hand to end on the radial sides of digits II to V (fig. 33a). The first lumbrical arises from the adjacent sides of the tendons for digits I and II, the second between those for II and III, the third between those for III and IV, and the fifth from those for IV and V. Each lumbrical reaches the radial side of the metacarpophalangeal joint where it crosses the palmar aspect of the deep transverse ligament of the hand. The muscle now changes into an aponeurotic and resistant membrane which blends distally with the corresponding dorsal extensor expansion at about the proximal half of the first phalanx.

Nerve supply: The first lumbrical is innervated by a branch from the median nerve ramus to the radial side of the index. The second lumbrical is also supplied by the median nerve, but through its ramus

for the adjacent sides of the index and middle finger. The third is innervated by both the median and the deep branch of the ulnar nerve; the median supplies it through its ramus to the ulnar side of the middle finger and the ulnar by the continuation of its ramus to the adductor pollicis and contrahens II. The fourth lumbrical receives its innervation from the deep ulnar nerve by the continuation of its ramus to contrahens V.

Function: They are all flexors of the metacarpophalangeal joints.

DEEP SERIES, SUPERFICIAL LAYER

The layer of contrahentes is represented by three muscles, namely, to the first, second, and fifth digits. There is no contrahens to the fourth digit.

M. adductor pollicis (fig. 34): This is a broad, thin, and triangular muscle whose origin corresponds to approximately the midline of metacarpale IV. It is superficial to the contrahens indicis and arises by muscular fibers from the palmar base of metacarpals II and III, capitate, and the ligamentous bindings of these bones. Fibers of the muscle come also, through a fine resistant aponeurotic lamina, from a sagittal septum attached to the palmar side of the fourth metacarpal shaft. The carpal bundles pass distolaterally, while those of metacarpal origin follow an increasingly horizontal direction. The insertion is by fleshy fascicles on the ulnar sesamoid of the first digit and the same side of the base of the first pollical phalanx. No separate oblique and transverse heads are to be found, but the radial border of the muscle is considerably thicker than the rest. Sirena (1871) also found the muscle not divided into oblique and transverse heads. He assigns the insertion to the whole length of the inner margin of the first pollical phalanx.

Nerve supply: By a branch of the deep ulnar nerve.

Function: Adductor of the pollex.

M. contrahens indicis: This is similar to but smaller than that for the first digit, under cover of which it lies (fig. 34). Its origin is from the palmar aspect of the third metacarpal base and capitate; more distally its fibers arise from the sagittal septum to the fourth metacarpal by means of the same aponeurotic lamina already described with the adductor pollicis. They all converge to the space between the heads of metacarpals II and III, which is crossed on the dorsal side of the corresponding deep transverse metacarpal ligament. The muscle ends on the ulnar side of the base of the proximal phalanx of digit II. Sirena (1871) calls this muscle *m. adductor indicis obliquus.*

Nerve supply: The same branch of the ulnar nerve which also innervates the adductor pollicis and the third lumbrical.

Function: Adducts the second digit.

M. contrahens digiti quinti: This is smaller than either of the other two members of this layer (fig. 34). Its origin is by fleshy fibers from the palmar aspect of the fourth metacarpal base and the adjacent surface of the hamate. Other fibers join the muscle from the sagittal septum to metacarpale IV, but these do not have a horizontal direction as those of the other two contrahentes. All its fascicles run distomedially and cross the dorsal side of the deep transverse metacarpal ligament joining the heads of metacarpals IV and V. They end on the radial side of the first phalanx base and corresponding articular capsule of V. Sirena (1871) found a similar contrahens digiti quinti in *Alouatta fusca.*

Nerve supply: The deep ulnar nerve.

Function: Adduction of the fifth digit.

DEEP SERIES, DEEP LAYER

M. flexor pollicis brevis, caput profundum (figs. 33a, 34): I was able to find in both hands of one of my male specimens what I believe to be a modification of this muscle. It is represented by a small but clearly identifiable muscle arising on the ulnar half of the first metacarpal base and ligaments of the adjacent joint. Its fleshy bundles are inserted on the ulnar side of the first metacarpal shaft. It lies completely under cover of the ulnar head of m. flexor pollicis brevis and is innervated by a twig from the deep ulnar nerve.

Mm. interossei: These muscles are arranged into four dorsal and three palmar interossei both in *Alouatta seniculus* (fig. 33) and *Alouatta fusca* (Sirena, 1871). Every dorsal interosseous originates from the adjacent sides of the metacarpals between which it is located (fig. 33a). Its fibers end on the expansion of the extensor tendon to the finger on whose metacarpal the interosseous takes the more extensive origin. The ventral interossei arise from only one metacarpal (fig. 33a). Their insertion is on the extensor expansion of the finger on whose metacarpal they arise.

The first dorsal interosseous lies between the first and second metacarpal bones and is formed by a radial head with fleshy origins from the dorsal half of the ulnar side of the shaft and base of metacarpale I and an ulnar head, of more extensive origin, from the entire radial half of the base and shaft of metacarpale II. The large single belly crosses the radial side of the second metacarpophalangeal joint where some of its deep fibers are anchored. The insertion is on the same side of the corresponding dorsal extensor expansion proximal to the first lumbrical. The second dorsal interosseous originates from the second and third metacarpals. It is also formed by two heads. The radial head arises from the dorsal half of the ulnar side of the second metacarpal shaft and base. The larger ulnar head has its

fibers originating from the whole radial half of the shaft and proximal end of the third metacarpal. The common belly flattens against the radial side of the third metacarpophalangeal joint where some fibers are inserted. It ends on the radial aspect of the dorsal extensor expansion of digit III proximal to the tendon of the second lumbrical. The third dorsal interosseous is also a double-headed muscle. It lies between the third and fourth metacarpals and is the mirror image of the second dorsal interosseous. Its larger radial head arises from the entire ulnar half shaft and base of metacarpale III. The ulnar head originates only from the dorsal half of the radial side of the shaft and proximal end of metacarpale IV. The muscle passes distally against the ulnar side of the third metacarpophalangeal joint on whose capsule some of its fibers attach. Insertion is on the ulnar side of the dorsal extensor expansion to the third digit. The fourth dorsal interosseous has an arrangement similar to that of the previous muscle. Its radial head is also larger and arises from the entire ulnar half of the shaft and base of the fourth metacarpal. The less developed ulnar head takes origin on the dorsal half of the radial side of the fifth metacarpal shaft and base. The muscle runs distally against the ulnar side of the capsule of the fourth metacarpophalangeal joint to which it gives some fibers. The insertion is on the dorsal extensor expansion to the fourth digit.

The first palmar interosseous occupies only the ulnar half of the second intermetacarpal space. It arises from the ventral half of the ulnar side of the shaft and base of metacarpale II. The fibers run distally and the muscle flattens against the ulnar aspect of the capsule of the second metacarpophalangeal joint. Some fibers end here, but most of them are inserted on the ulnar side of the dorsal extensor expansion to the second digit. This muscle is of the same approximate size as the third palmar interosseous. The second is the best developed of the three and occupies only the radial half of the third intermetacarpal space. Origin is from the palmar half of the radial side of shaft and base of metacarpale IV. It lies against the radial side of the fourth metacarpophalangeal joint on whose capsule some of its fibers end. The muscle blends with the dorsal extensor expansion of the radial side of digit IV proximal to the third lumbrical. The third palmar interosseous is on the radial half of the fourth intermetacarpal space and originates from the palmar half of the radial side of the shaft and base of metacarpale V. The muscle crosses the radial aspect of the last metacarpophalangeal joint. Some of its fibers end abductors and the here, but the majority are inserted on the dorsal extensor expansion to the fifth digit above the fifth lumbrical ending.

Nerve supply: The deep ulnar nerve.

Function: Every interosseous is an extensor of the metacarpo-

phalangeal joint of the corresponding digit. This is brought about by the insertion on the dorsal extensor expansion proximal to the ending of the lumbrical and after crossing the dorsal side of the deep transverse metacarpal ligament. In addition, the dorsal interossei are abductors and ventral adductors. In relation to the zygodactylous grasp, the second palmar interosseous is the best developed of the three.

M. opponens digiti quinti (=*opponens digiti minimi of N.A.*): It is the deepest of all the hypothenar muscles and occupies the radial side of the ventral aspect of the fifth metacarpal where it is inserted on the whole ventral shaft up to the head (fig. 34). Its fibers originate on the palmar aspect of the fifth metacarpal base and nearby hamate.

Nerve supply: Deep branch of the ulnar nerve.

Function: Medially rotates metacarpale V.

Comparative anatomy of the hand muscles.—The intrinsic thumb muscles in the spider monkey are sometimes well differentiated with an arrangement comparable to that of the howler with which they coincide even in the presence of a flexor pollicis brevis profundus. More often they are rudimentary in this genus (see Straus, 1942, and Straus, unpublished data). Senft (1907) found no abductor brevis or opponens to the thumb and the corresponding flexor represented only by a broad musculotendinous strand between the flexor retinaculum and the head of metacarpale I and the rudimentary phalanx. The thenar muscles in *Brachyteles* form only an undifferentiated mass (Hill, 1962), but in *Lagothrix* (Robertson, 1944) they are like those of *Alouatta*. The abductor pollicis brevis of the capuchin monkey studied by Senft (1907) was fused with the flexor brevis to the extent that he regarded the first as merely a part of the second. This went from the flexor retinaculum to its usual phalangeal ending, but Senft (1907) does not say whether or not it had two heads. He did not find an opponens pollicis. Other observations in *Cebus* (Straus, unpublished) report a pattern of thenar muscles like that of the howler.

A relatively well-developed palmaris brevis occurs in *Lagothrix* (Robertson, 1944) and *Cebus* (Straus, unpublished), but was not found in *Ateles* (Straus, unpublished). The observation of Sirena (1871) of one such muscle on the thenar side of *Alouatta* remains unique.

The three hypothenar muscles of *Ateles* (Senft, 1907; Straus, unpublished) match quite accurately the features of those in *Alouatta*, but Senft (1907) apparently did not find the opponens. The abductor of the fifth digit in *Brachyteles* is said to be bicipital and one of these heads is supposedly homologous to the short flexor of the fifth digit, as described by Robertson in 1944 (see Hill, 1962). Its opponens to V is feeble (Hill, 1962). The three muscles in *Lagothrix* (Robertson, 1944) are just like those in the howler. In *Cebus* (Senft, 1907) the

abductor digiti quinti extends partially connected with the flexor from the pisiform to the first phalanx. Senft (1907) thinks that because of the volar position of the abductor of the fifth digit in the capuchin monkey, it is, in this case, more a flexor than an abductor. The flexor of this digit goes from the flexor retinaculum to the first phalanx. The lack of separation between the two muscles has also been found in other specimens of *Cebus* (Straus, unpublished) where, nevertheless, the opponens was present with a similar arrangement to that I have found in *Alouatta.*

The four lumbricals offer no significant differences in any of these five platyrrhines.

The contrahentes of *Ateles* were studied by Forster (1916b) and, more recently, but in less detail by Jouffroy and Lessertisseur (1959). Forster (1916b) indicated the presence of a superficial layer formed by contrahens II and V arising from an aponeurotic raphe extended obliquely from the base of metacarpale III to the head of the fifth. The first of these two muscles was inserted on the ulnar base of the first phalanx of digit II, the second on the radial base of the first phalanx of digit V. He found contrahentes IV and I deep to the first two, but with similar origins. Insertion of contrahens IV was on the radial base of the first phalanx of digit IV, the adductor pollicis on the fore end of the rudimentary metacarpale I. Jouffroy and Lessertisseur (1959) describe the existence of additional transverse bundles running between the heads of the metacarpals. Straus (unpublished) found, contrariwise to Forster (1916b), the adductor of the thumb in a superficial layer together with m. contrahens V from which it is ill separated by a raphe extending from the base to the head of the third metacarpal. M. contrahens II is large and deep to I, ending on the ulnar base of the first phalanx digit II. He did not see a contrahens IV (Straus, unpublished). In his account of *Brachyteles,* Hill (1962) talks only of a contrahens II with insertion on the radial side of digit III, but when covering the interossei he indicates the presence of a preaxially located belly, the abductor indicis, inserted on the medial margin of the extensor tendon of the index. The contrahentes of the woolly monkey (Robertson, 1944) are represented by a large m. adductor pollicis arising from the carpus and a raphe extended from the center of the hand to the fifth metacarpophalangeal articulation. It covers a contrahens II called by Robertson (1944) *m. adductor indicis proprius,* which has what I regard as an anomalous insertion to the ulnar side of the dorsal extensor expansion, although he says that it sometimes takes place on the lateral side of the proximal phalanx. If by "lateral" he means "radial," this attachment would still be peculiar. There is, in addition, a muscular bundle whose origin is from a central tendon on the carpus just medial to

and in the same plane as contrahentes I and II. Robertson (1944) describes it as branching off distalward into three heads: (1) One joins the tendon of what appears to be a volar interosseous with which it blends on the radial border of the dorsal extensor expansion of digit V. This head sends a group of fibers to the radial head of metacarpale V and may be regarded as a contrahens V with anomalous attachments. (2) A second head joins an interosseous tendon which meets the ulnar side of the dorsal extensor expansion on digit IV. (3) The third head, which perhaps represents contrahens IV, joins also an interosseous tendon to be continuous with the dorsal extensor aponeurosis on the radial side of digit IV. This kind of contrahens ending is, I repeat, peculiar. A full set of contrahentes seems to be the rule in *Cebus* (see Forster, 1916b; Jouffroy and Lessertisseur, 1959; Straus, unpublished), but the pattern has been variously described. Forster's observations (1916b) fit the type b) discussed by Jouffroy and Lessertisseur (1959) and that of the French authors corresponds to their a) model. Straus' findings (unpublished) appear to fall in between these two.

According to Forster (1916b), the ventral interossei of the spider monkey are double, one arising at each side of every metacarpal base and shaft I to V to end, respectively, on the ulnar and radial aspects of the corresponding metacarpophalangeal articular capsules. The dorsal interossei, on the other hand, are said to have the common bicipital arrangement with digit III as the central axis. Jouffroy and Lessertisseur (1959) describe five dorsal interossei in *Ateles:* one with two heads in the first intermetacarpal space; another two-headed dorsal interossei in the second; two bicipital muscles in the third, one going to the ulnar side of digit III, the other to the radial side of IV; and, finally, a single-headed dorsal interosseous along the ulnar side of IV. This disposition corresponds to their paraxonique type and is illustrated in their figure 3. Straus (unpublished) speaks of seven interossei in the right hand of one *Ateles geoffroyi*, four bicipital dorsals and three ventrals, the last arising from a single metacarpal. He has found the actual separation between the dorsals and ventrals not always complete, the first ending mostly on the corresponding phalanges with some fibers reaching the dorsal extension expansion, whereas the second has the reverse kind of insertion. This pattern is like that of *Alouatta*. The information about *Brachyteles* does not lend itself easily to the kind of comparison I am interested in making because Hill (1962), who is the only source for these muscles in the woolly spider monkey, does not clearly explain the origins of what he calls dorsal and volar interossei. Robertson (1944) was apparently faced with an extremely complicated pattern of interosseous muscles in *Lagothrix*. The situation is probably similar to that of

Alouatta, and the spider monkey as observed by Straus (unpublished), but I cannot be sure of this due to Robertson's rather unclear description of these muscles. Straus (unpublished) studied them in the left side of one juvenile *Cebus malitiosus* (= *Cebus albifrons*). He found four dorsals and four ventrals. Of the last, the one on the radial side of the second intermetacarpal space he regards as merely a subdivision of the second dorsal. Only the first and the third dorsal are bicipital and the fourth ventral has an additional proximal origin from the hamate process and the transverse carpal ligament. All the interossei contribute definite expansions to the extensor aponeurosis.

Muscles of the Lower Extremity

Dorsal Musculature

Coxofemoral Group

PREPELVIC

M. iliopsoas: This muscle is formed by the iliacus and the psoas major, each with a separate origin but with a common insertion (fig. 20).

M. psoas major is a fleshy thick column extending along the side of the lumbar spine, across the pelvis major to the lesser trochanter of the femur. The muscle arises by a series of fleshy arcades anchored to all of the intervertebral disks of the lumbar region. In all specimens the more caudal fibers invariably originate also from the body of the last lumbar vertebrae. The costal processes of the third to the fifth or sixth vertebrae contribute fleshy digitations to the dorsal surface of the psoas major. The large fusiform belly lies in the angle formed by all the lumbar bodies and their costal processes. It has two frontal cleavages; the ventral and cranial one allows for the formation and passage of the lateral femorocutaneous nerve, the dorsal and distal is traversed by the femoral nerve and its roots.

M. iliacus is formed by abundant fleshy fascicles coming from the entire iliac fossa and inner lip of the crest. Its bundles converge toward and join the dorsal surface of the psoas major. The combined iliopsoas fibers end on a strong tendon which begins within the muscle while it is still in the pelvis. The tapering musculotendinous belly forms the lateral floor of Scarpa's triangle and curves dorsally under the neck of the femur to a robust tendinous attachment on the tip of the trochanter minor. Sirena (1871) states that the origin of psoas major extends up to the body of L 1.

Nerve supply: The iliopsoas receives branches from L IV and L V (fig. 35).

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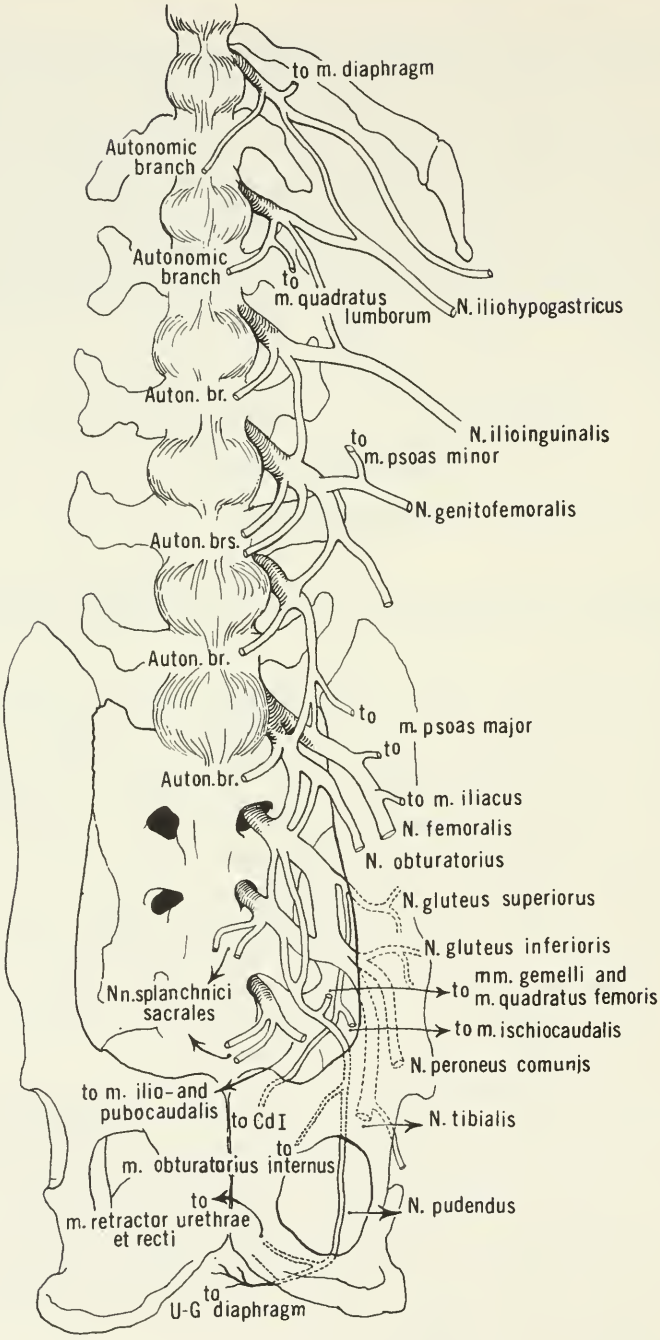


FIGURE 35.—Plexus lumbosacralis.

Function: The combined muscle produces flexion of the thigh on the hip as well as lateral rotation of the femur.

M. psoas minor: Fusiform and elongated, it extends between the higher lumbar vertebrae and the linea arcuata of the pelvis. It arises by mostly tendinous fibers from lumbar bodies 1 to 3 and the corresponding intervertebral disks. These fascicles are short, rapidly be-

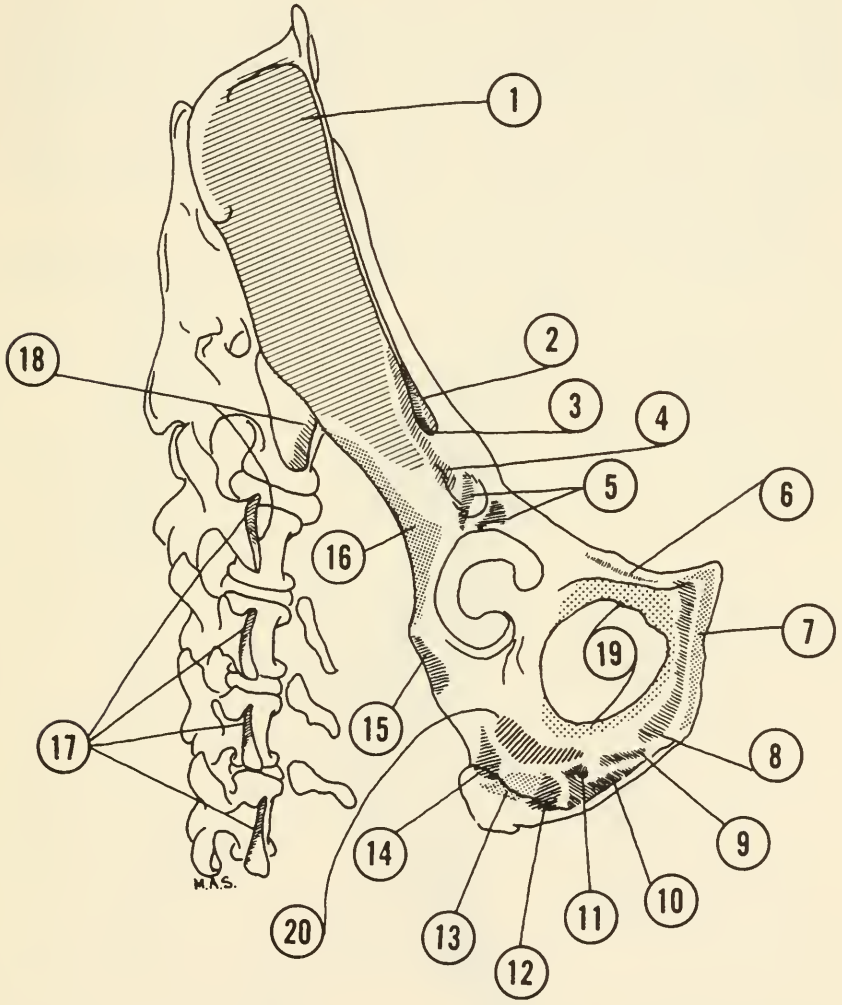


FIGURE 36.—Muscular attachments on the hip bone (1, m. gluteus medius; 2, m. sartorius; 3, m. tensor fasciae latae; 4, m. scansorius; 5, m. rectus femoris; 6, m. pectineus; 7, m. gracilis; 8, m. adductor longus; 9, m. adductor brevis; 10, m. adductor magnus; 11, m. semimembranosus; 12, m. semitendinosus; 13, m. biceps femoris; 14, m. gemellus inferior; 15, m. gemellus superior; 16, m. gluteus minimus; 17, m. gluteus maximus; 18, m. piriformis; 19. m. obturatorius externus; 20, m. quadratus femoris.

coming fleshy. In the female they did not extend caudally on both sides beyond the disk between L 2 and 3, and in all specimens the cranial bundles came from the disk between the last thoracic and first lumbar vertebrae. The psoas minor runs distally on the lateral side of the vertebral column under the medial lumbocostal arch. It changes into a shiny and strong tendon at the level of the fourth lumbar vertebrae, where it is medial to the psoas major. Further down in the pelvis it lies between that muscle and the iliac vessels, with a well-developed fascia transversalis intervening. As the psoas minor approaches its ending, the tendon broadens considerably and is now transversely flattened. Insertion is on the distal end of the linea arcuata (fig. 22). Sirena (1871) emphasizes the development of this muscle in *Alouatta* with relation to man. His findings agree with mine.

Nerve supply: A branch from the genitofemoral nerve (fig. 35).

Function: Bends the lumbar spine forward.

M. sartorius: A long and ribbon-like muscle found diagonally

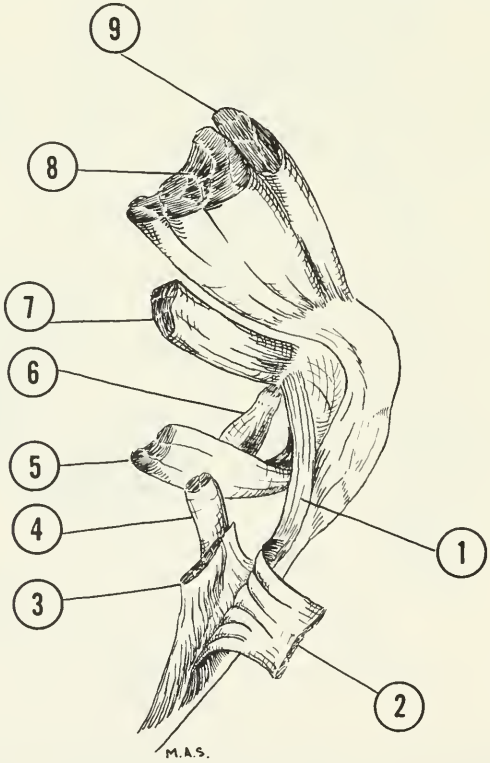


FIGURE 37.—Medial view of the knee (1, lig. collaterale tibiale; 2, m. sartorius; 3, m. gracilis; 4, m. semitendinosus; 5, m. semimembranosus; 6, m. gemellus medialis; 7, m. ischiocondyloideus; 8, m. vastus lateralis; 9, m. rectus femoris).

across the ventral aspect of the thigh from the innominate bone to the tibia. The origin is from the distal part of the acetabular border together with the tensor fasciae latae and scansorius (fig. 36). The fleshy fibers of the sartorius intervene here between these two muscles and the iliac insertion of the external oblique aponeurosis. The muscle passes distally over the quadriceps to the medial aspect of the knee where it lies over the endings of both m. gracilis and the semitendinosus. It now expands fanwise to be inserted on the proximal fourth of the medial aspect of the tibia (figs. 37, 38). Here, the highest sartorial fibers end at about 1.5 cm below the corresponding condyle. The muscle contributes to form the pes anserinus with the gracilis and

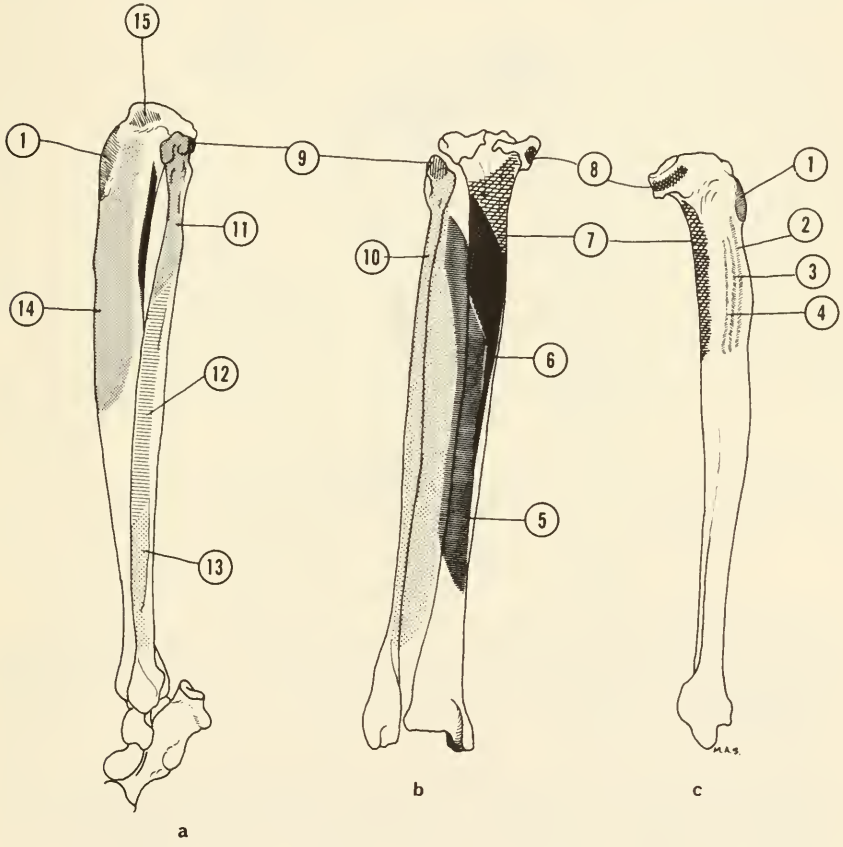


FIGURE 38.—Muscular attachments in the leg: *a*, lateral view; *b*, dorsal view; *c*, medial view (1, patellar tendon; 2, m. sartorius; 3, m. gracilis; 4, m. semitendinosus; 5, m. tibialis posterior; 6, m. flexor digitorum tibialis; 7, m. popliteus; 8, m. semimembranosus; 9, m. soleus; 10, m. flexor digitorum fibularis; 11, m. peroneus longus; 12, m. peroneus brevis; 13, m. peroneus digiti quinti; 14, m. tibialis anterior; 15, m. biceps femoris).

semitendinous. The saphenous nerve and artery pass between the distal part of these two muscles and the sartorius.

Sirena (1871) remarks that the origin is not from an anterosuperior iliac spine, but lower down on the anterior border of the coxal bone above what he calls the anteroinferior iliac spine. I have observed a well-defined though small eminence at this point. In other respects the muscle is said (Sirena, 1871) to be like that of man.

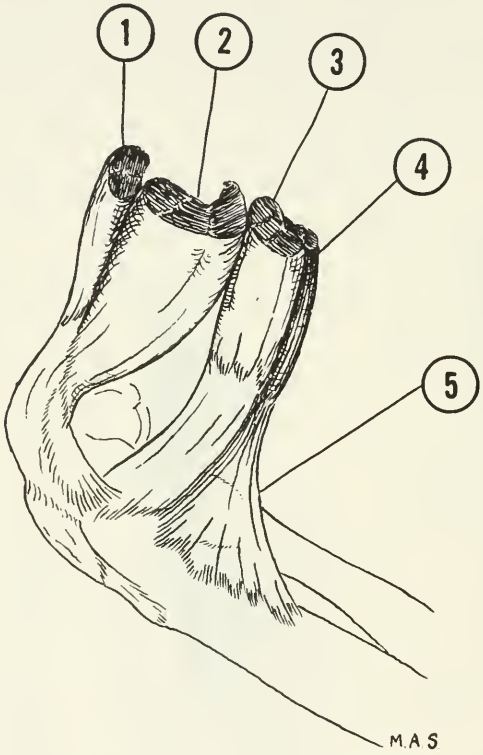


FIGURE 39.—Lateral view of the knee (1, m. rectus femoris; 2, m. vastus lateralis; 3, m. biceps femoris, caput longum; 4, m. biceps femoris, caput breve; 5, trigonum subtendinosum.

Nerve supply: Two branches of the femoral nerve reach the undersurface of the sartorius proximally. The saphenous nerve provides an additional branch to the deep aspect of its distal third.

Function: Flexes the femur on the hip bone. Also flexes the knee, and in this position it rotates the hind limb laterally, bringing it in abduction. This last effect is important in the quadrupedal arboreal movements of the animal when he carries these extremities partially flexed and abducted.

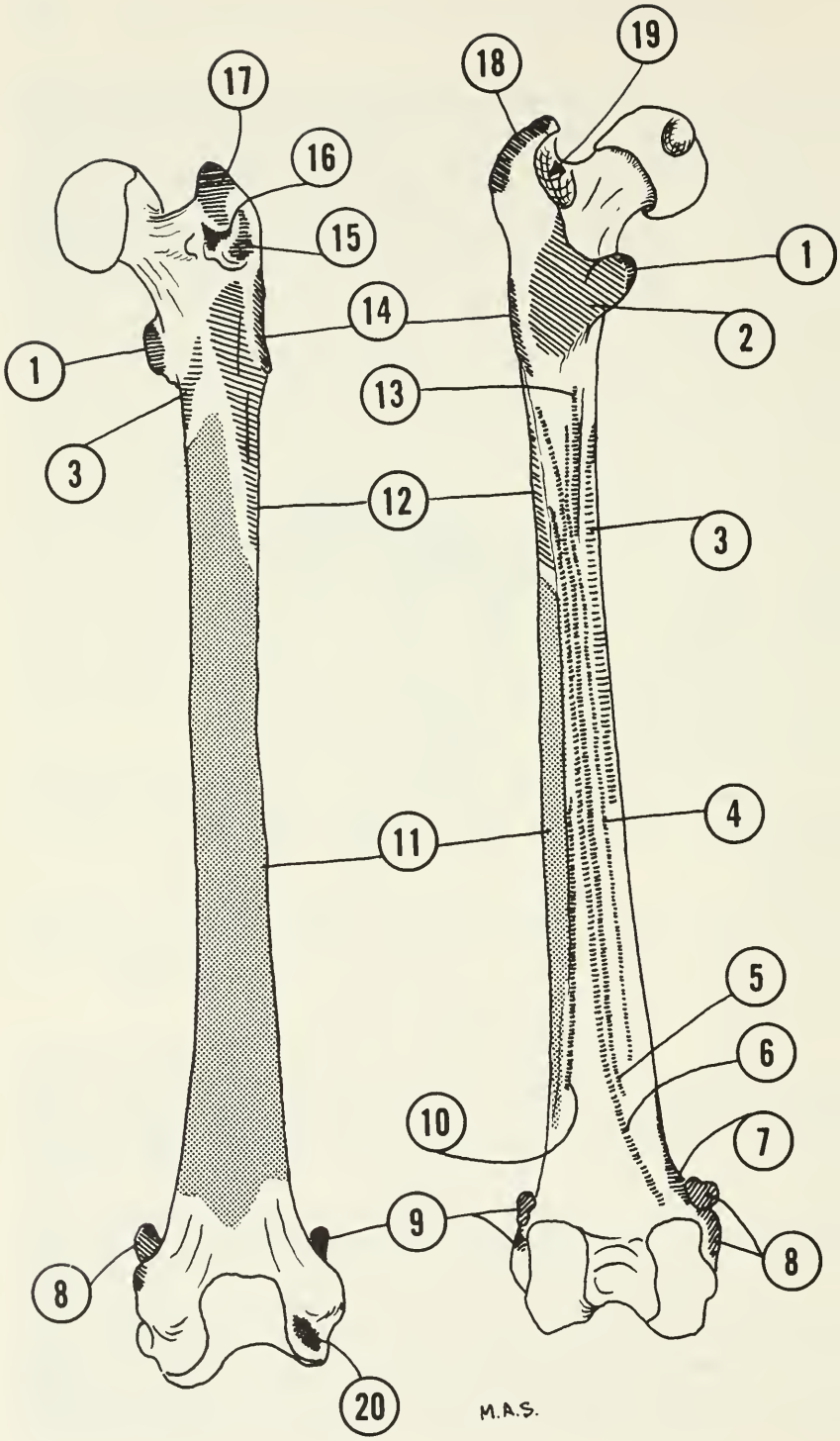
M. rectus femoris: A long muscle arising by two heads from the innominate bone and extending distally to the knee. A direct tendon is laterally compressed and has a lineal origin from the anteacetabular tubercle to the top of the acetabulum (fig. 36). It is thicker near the bone and after a short stretch gives origin to fleshy fibers. On a side view the tendon appears triangular, with the base corresponding to its origin and the apex to the continuation with the muscle. The reflected tendon is larger and laterally covered along its ventral margin by the direct tendon. Origin is from the cranial margin of the acetabulum (fig. 36), from where it runs distally for about 2 cm before being joined by the other head. The rectus femoris descends along the front of the thigh, flanked by the two vasti and covering the intermedius. Its fibers become tendinous near the knee and are arranged in two layers: (1) A superficial and larger group forms a short and rectangular tendon, most of whose fibers are inserted in the apex and both sides of the upper patellar border, the rest pass in front of this bone, beyond which they are firmly attached to the tibial tuberosity as the robust patellar tendon (figs. 37, 38, 39). (2) The deep group is smaller and forms a more reduced tendon which receives the fleshy and tendinous fascicles of vastus lateralis laterally and distally joins the vasti intermedius and medialis as they are inserted upon the patella and the articular capsule.

Sirena (1871) describes the direct tendon as being internal (medial?) to the external (lateral?) and reflected one. This is the reverse of my observations. According to him, the whole quadriceps is very well developed.

Nerve supply: The direct tendon receives two twigs from the femoral nerve, one of them very small, before joining the reflected part. Another branch of the femoral enters the undersurface of the rectus femoris at the junction of the upper and middle thirds.

Function: It flexes the hip and extends the knee.

Mm. vasti: M. vastus lateralis is the largest of all the components of the quadriceps and, as its name implies, lies on the lateral side of the thigh. Its fleshy fibers have an aponeurotic and bony origin. They come from the anterior aspect of the lateral intermuscular septum in front of the insertion of both the gluteus maximus and the short bicipital head on this fibrous partition, and from the almost entire lateral part and the upper fifth of the anterior femoral surfaces (fig. 40). The origin of vastus lateralis reaches the intertrochanteric line on the ventral surface of the bone. These fascicles are all directed distomedially and contribute to cover the vastus intermedius. Those closer to the limb axis reach the lateral border of both terminal tendons of the rectus femoris. Further away, fibers become aponeurotic before a similar insertion, and still more distal ones, with respect to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the axis, pass in front of the articular capsule, reinforce it and are attached to the anterior aspect of the lateral tibial condyle in front of the insertion of m. biceps (fig. 39).

M. vastus medialis occupies the medial side of the ventral compartment of the thigh ,separated by the median intermuscular septum from the adductor group of muscles. It arises from the whole extent of this aponeurotic partition and on the femur from the linea aspera over the upper half of its medial lip up to the intertrochanteric line, where its origin extends a little onto the anterior face of the bone (fig. 40). The fibers of the vastus medialis are oriented distolaterally. Those close to the femoral axis are inserted directly on the medial edge of the deep terminal tendon of the rectus femoris, while fibers further away from that axis become tendinous and pass in front of the articular capsule to end on the ventral border of the medial tibial condyle and the patellar tendon (fig. 37).

M. vastus intermedius is entirely covered by the other three components of the quadriceps. Origin is from the entire ventral surface of the femur, except on those areas from which the other two vasti arise (fig. 40). Its fibers run distally and are partially split at their distal third by an incomplete and frontally arranged cleavage. In this manner those arising from the proximal two-thirds of the bone cover those coming from the distal third. Both portions remain connected along their medial borders where the cleavage plane is not well defined. I regard the covered portion as the m. articularis genu. The vastus medialis attaches to the whole upper border of the patella deep to the terminal tendons of the rectus femoris. Its deeper fibers are continuous with the fibrous ones of the articular capsule. The findings of Sirena (1871) in *Alouatta fusca* call for no special comment.

Nerve supply: The vasti are innervated by the femoral nerve. Its branch to vastus lateralis is particularly large.

Function: Extension of the knee.

Comparative anatomy of the prepelvic coxofemoral group.—Accessible information about this group of muscles in the five cebids under consideration is found only in Hill's work (1960, 1962). There seem to be little differences among them. The sartorius muscles of the woolly (Hill, 1962), woolly spider (Hill, 1962) and capuchin monkey (Hill, 1960) appear to be similar to that of *Alouatta*. Hill (1962)

Figure 40.—Muscular attachments of the femur (1, m. iliopsoas; 2, m. quadratus femoris; 3, m. vastus medialis; 4, m. adductor longus; 5, m. adductor brevis; 6, m. ischiofemoralis; 7, m. ischiocondyloideus; 8, m. gastrocnemius, caput mediale; 9, m. gastrocnemius, caput laterale; 10, m. biceps femoris, caput breve; 11, m. vastus intermedius; 12, m. vastus lateralis; 13, m. pectineus; 14, m. gluteus maximus; 15, m. scansorius; 16, m. gluteus minimus; 17, m. gluteus medius; 18, m. piriformis; 19, fossa trochanterica; 20, m. popliteus).

explains that the relations of the muscle in *Brachyteles* are the same as in *Ateles,* but its transverse dimensions are more reduced. The two woolly monkeys have a bicipital rectus femoris and three well-differentiated vasti (Hill, 1962). *Ateles* is not so thorough in the independence of its vasti (Hill, 1962). *Cebus* (Hill, 1960) has not a bicipital femoral rectus, but in other respects the resemblance to *Alouatta, Brachyteles,* and *Lagothrix* is strong.

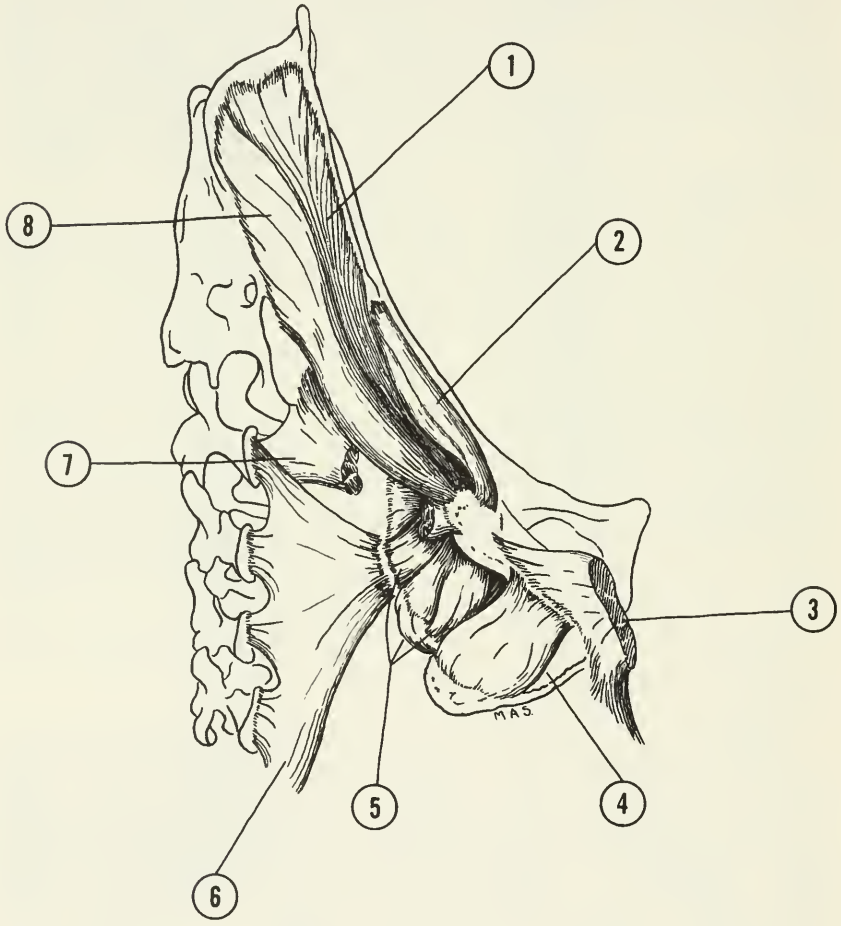

FIGURE 41.—Muscles of the gluteal region (1, fibers of m. gluteus medius arising from the dorsally facing portion of the gluteal plane; 2, m. scansorius; 3, terminal portion of m. gluteus maximus; 4, m. quadratus femoris; 5, mm. gemelli and m. obturatorius internus; 6, m. ischiocaudalis; 7, m. piriformis, sectioned; 8, fibers of m. gluteus medius arising from the laterally facing part of the gluteal plane).

POSTPELVIC

M. gluteus minimus: The smaller of the gluteal muscles is triangular, and its fleshy, firm origin from the margin of the greater sciatic notch and the sciatic spine corresponds to the base of the figure. It occupies the distal part of the gluteal plane and the prominence of the glenoid cavity (fig. 41). The belly passes in front of the iliofemoral capsule to which it is connected by fibrous strands. Insertion is on the ventral border of the trochanter major between the gluteus medius above and the scansorius below (fig. 40). M. gluteus minimus is separated from the piriformis by the sciatic trunk, the gluteal and posterior femorocutaneous nerves, the pudendal nerve accompanied by the internal pudendal vessels, and the nerve to the gemelli and quadratus femoris.

According to Sirena (1871), this muscle is better developed than the other two glutei and very difficult to separate from the medius. Its origin, insertion, and relations otherwise correspond with what I found in the red howler. Waterman (1929) assigns a double origin to m. gluteus minimus (see her figure 3) in *Alouatta,* from the distal part of the acetabular border and the margin of the greater sciatic notch. The former probably corresponds to m. scansorius as indicated by Hill (1962).

Nerve supply: A branch from the superior gluteal nerves enters the muscle on its superficial aspect near the cranial border.

Function: A medial rotator of the femur.

M. gluteus medius: It is the largest of the three gluteal muscles, although not very much more so than the maximus (fig. 41). Its fleshy fibers originate from an extensive area which includes (1) the entire gluteal plane, except for a small portion occupied by the scansorius, and (2) the whole peripheral margin of this plane, except the part corresponding to the sciatic notch and that of the acetabular border taken up by the scansorius and tensor fasciae latae (fig. 36). Additional fleshy fascicles are supplied from the gluteal aponeurosis near the iliac crest. The voluminous belly is directed distally under partial cover of the gluteus maximus and tensor fasciae latae. The ventral margin, formed initially by tendinous fibers, is closely related to m. scansorius, and the caudodorsal to the piriformis, as this muscle leaves its origin and goes to the trochanteric fossa. The gluteus medius can be clearly separated from these two neighboring bellies, although some fibers of the piriformis join the gluteal tendon near the vertex of the large trochanter. M. gluteus minimus is completely covered by the medius. All bundles of the medial gluteus converge upon a central band-like tendon, those coming from the laterally facing part of the gluteal plane end on the dorsocaudal aspect and lateral margin of the tendon; fibers from the rest of this plane (and these are by

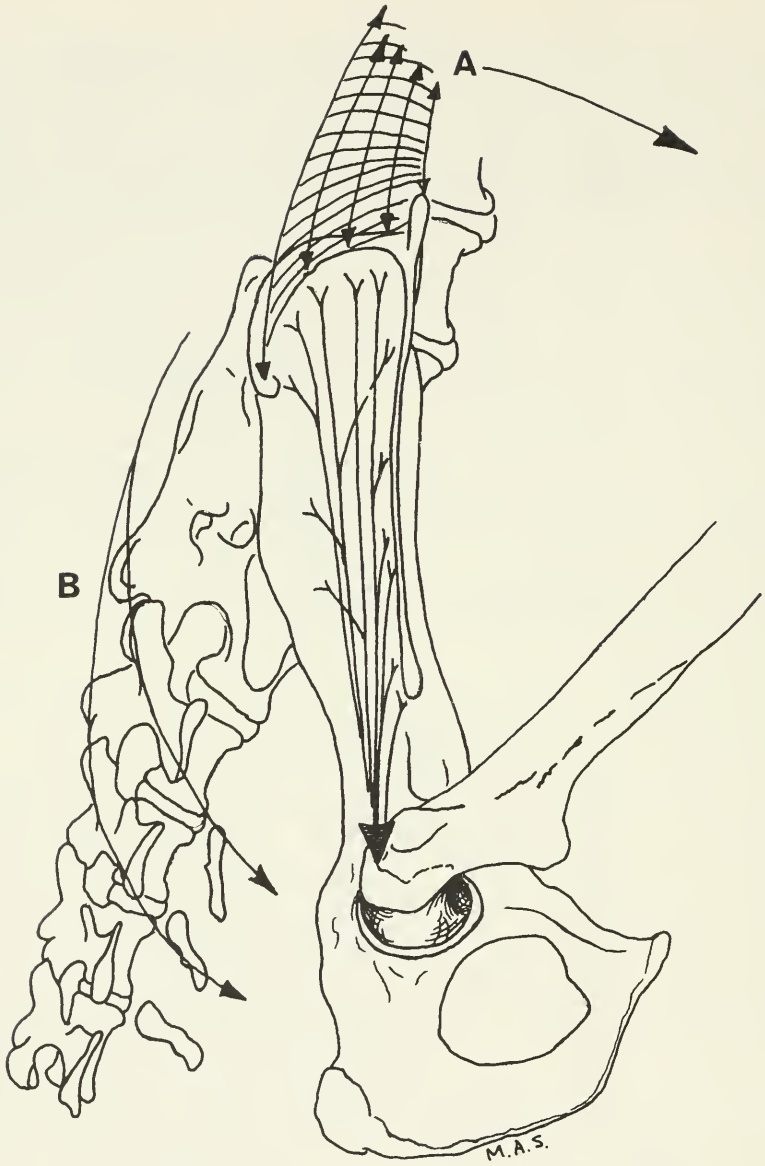

FIGURE 42.—a, By the action of the erector spinae the vertebral column and the pelvis are transformed into a rigid column that tends to tilt forward due to its own weight and those of the skull and enlarged neck structure. The insertion of the erector spinae on the iliac crest extends this effect down to the iliofemoral joint on whose transverse axis the tilting would take place. b, The gluteus medius pulls the ilium and therefore the trunk back.

far the most abundant) attach to its cranioventral aspect and medial border. The part of the tendon not covered by muscle is very short. Insertion is on the ventral slope of the greater trochanter, above the endings of the gluteus minimus and scansorius (fig. 40).

Sirena (1871) says that the origin extends to the transverse processes of the first caudal vertebrae and the last portion of the sacral crest. There is no difference in the insertion.

Nerve supply: A branch from the superior gluteal nerve reaches the muscle on its deep surface and near the origin from the posterior margin of the ilium.

Function: When the pelvis is fixed, the gluteus medius is a lateral rotator of the thigh by means of its fibers arising on the laterally directed part of the iliac blade (fig. 42). The contraction of these same bundles will produce some rotation of the pelvis if the femur is the fulcrum. Medial gluteal fibers with origin on the dorsally facing area of the gluteal plane would help to flex the thigh on the pelvis when the leg is extended as in the rare occasions when the animal stands on its hind limbs. On the other hand, if the thigh is flexed and fixed in that position as happens in squatting, contraction of these same fibers would tend to prevent forward tilting of the pelvis and trunk in general. Waterman (1929) has already mentioned the importance of these fascicles in *Cebus* when the animal squats. She did not account, however, for the pronounced development of the horizontal part of the iliac blade in *Alouatta*. It seems to me reasonable to think that this osteological character might be related to the function of the gluteus medius of this animal in maintaining the trunk semierect when sitting on its haunches. According to Carpenter (1934), there is considerable variability in the posture of the howlers. He observed that one of their frequent postures was that of resting in a sort of squatting position. In such a stance the trunk tends to bend forward as an arch due to its own weight. This is prevented by the action of the erector spinae, whose contraction transforms the spine and the whole trunk into a rather rigid column on top of which the head and neck are balanced (fig. 42). In consequence of this, the body tends to tilt forward at the hip joint. The enlarged hyolaryngeal apparatus at the cranial end of the rigid column enhances this tendency. It is the contraction of those fibers of the middle gluteus with origin on the horizontal area of the gluteal plane that pulls the pelvis and therefore the whole trunk backward, thus preventing the forward tilting (fig. 42).

M. tensor fasciae latae: This muscle is found right where the boundaries of three regions meet, the gluteal, inguinal, and femoral (fig. 43). It is superficial, weak, and lies in a narrow compartment formed within both the gluteal aponeurosis and the fascia lata, these

two structures continuing one into the other. The tensor fasciae latae arises by fleshy fibers from the caudal part of the acetabular border between m. scansorius and m. sartorius (fig. 36). Most of its fibers come from the gluteal aponeurosis. The tensor is thicker above than below, where it expands ventrolaterally, reaching down to approximately the junction between the proximal and intermediate thirds of the thigh. The muscle ends on the fascia latae. There is no well-

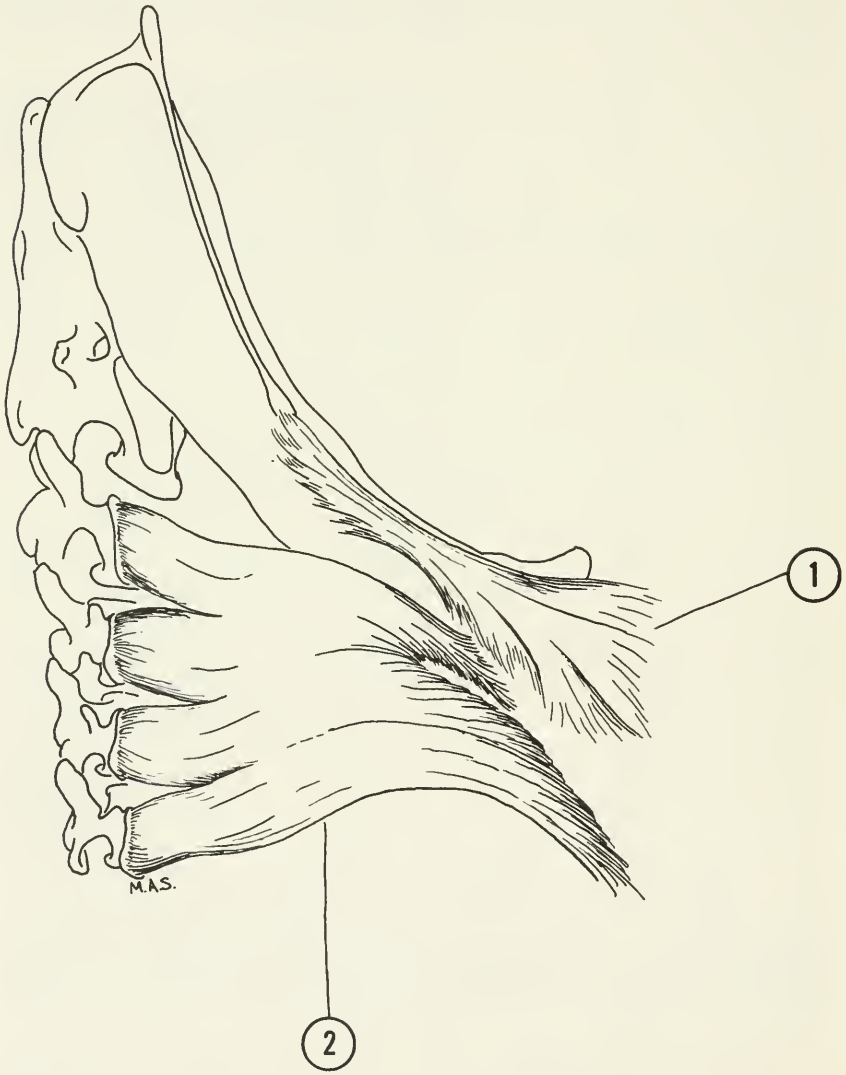

FIGURE 43.—Gluteal region (1, m. tensor fasciae latae; 2, m. gluteus maximus).

defined iliotibial tract. Waterman (1929) indicates that this muscle is present in the howler but reduced in size. *Alouatta fusca* (Sirena, 1871) does not differ from the red howler in this respect.

Nerve supply: Branches of the superior gluteal nerves reach the muscle after emerging from below the ventrocranial margin of m. gluteus medius and traveling below the scansorius.

Function: That which is implied by its name.

M. scansorius: It is a large, fusiform muscle found deep to the tensor fasciae latae between the gluteus medius dorsally and the origin of sartorius ventrally (fig. 41). Its size is about one-third that of the medial gluteus and larger than the minimus. The scansorius arises by strong fleshy fibers from (1) the lower third of the acetabular border together with the tensor fasciae latae and the sartorius, and (2) the antacetabular tubercle (fig. 36). Some of its fibers slightly invade the gluteal plane. The muscle passes distally across the iliofemoral articulation and is inserted by a strong and short tendon to a facet on the lateral surface of the trochanter behind its ventral border (fig. 40). A similar scansorius is present in *Alouatta fusca* (Sirena, 1871). Hill (1962) correctly points out that what Waterman (1929) describes as an origin of gluteus minimus from the acetabular border is actually the scansorius, but he goes on to say that the insertion is on the digital fossa together with the piriformis.

Nerve supply: A branch from the superior gluteal nerve supplies the muscle on its deep surface.

Function: It is probably the same as that described for the gluteus medius when the animal squats; otherwise the muscle is a medial rotator of the thigh.

M. gluteus maximus: It is a flat, extensive, and triangular sheet formed by thick muscular bundles which from their origin on the proximal caudal vertebrae converge to the lateral side of the upper third of the femur (fig. 43). Its fleshy fibers arise from the costal processes of Cd 1 to 4 (fig. 36) and from the gluteal aponeurosis which covers the whole region. As in the case of the howlers of Sirena (1871), the fibers from Cd 3 and 4 (distocaudal fibers) have a craniolateral direction and those from Cd 1 and 2 (proximocaudal fibers) are oriented caudolaterally. The insertion of the first is on the proximal half of the fascia lata along the lateral margin of the thigh. The proximocaudal bundles are attached directly to the bone by means of a tendon in whose formation all gluteal fibers participate. The muscle thus has a bipennate arrangement. The cranial border of the belly adjoins the tensor fasciae latae, and the caudal is intimately connected by fibrous tissue to the long head of m. biceps femoris. The two muscles are easy to differentiate by their nerve supply, and careful dissection allows their separation. A gluteal

rugosity in the upper fourth of the lateral side of the femoral shaft corresponds to the femoral insertion of gluteus maximus (fig. 40). It is continuous caudally with the lateral line of bifurcation of the linea aspera.

Waterman (1929) points out that the muscle has no origin from the iliac blade. My description does not differ from that of Sirena (1871).

Nerve supply: The inferior gluteal nerve reaches the deep surface of the muscle closer to the origin than to the insertion.

Function: It abducts the thigh from the tail and vice versa. It probably has no significant effect on extending the limb, this action being dependent on the strong hamstring muscles.

M. piriformis: This muscle has no intrapelvic part and is found entirely in the gluteal region deep to the gluteus maximus and just caudal to the medius with which it covers the minimus (fig. 41). Origin is from the tip of the costal process of the first caudal vertebra and the free lateral margin of the sacrum. The fleshy fibers converge toward the posterior slope of the greater trochanter as a round belly. The sciatic trunk with the associated nerve and vessels passes deep to the muscle. Insertion is on the dorsal margin of the femoral trochanter (fig. 40) and by some fibers on the tendon of the gluteus medius. Sirena (1871) did not recognize the sacral and caudal origins of the piriformis, attributing its origin to only the margin of the sciatic notch. He also noted the fact that the muscle has no intrapelvic part.

Nerve supply: Nerve to the piriformis.

Function: Lateral rotation of the thigh.

M. biceps femoris, caput brevis: This portion of the biceps will be treated together with its long component in a following section.

Comparative anatomy of the postpelvic coxofemoral group.—The arrangement of the postpelvic muscles in the howler does not appear too different from the patterns found in the four other large cebids, excluding the capuchin. The studies of Bodini (1965) on the lower limb of *Alouatta, Ateles,* and *Lagothrix,* of Hill (1962) on *Brachyteles,* of Klaatsch (1900) on *Ateles* and *Lagothrix,* and of Waterman (1929) in *Alouatta* sustain this generalization. A tensor fasciae latae is not differentiated, however, in the spider (Bodini, 1965; Hill, 1962), woolly (Bodini, 1965; Hill, 1962) and woolly spider monkey (Hill, 1962), but it is found in *Cebus* where the muscle is better developed than in *Alouatta* (Bodini, 1965). The gluteus maximus of *Ateles* (Bodini, 1965; Hill, 1962), *Brachyteles* (Hill, 1962), and *Lagothrix* (Bodini, 1965; Hill, 1962) appears as an extensive triangular sheet with fleshy fibers arising from the proximal caudal vertebrae and undersurface of the gluteal aponeurosis up to the iliac crest.

Bodini (1965) has found in the spider and woolly monkeys a clear origin of the muscle from the acetabular margin. The insertion in both animals is on the trochanter major according to Bodini (1965), but Hill (1962) attributes such termination only to *Ateles*. He says that in *Lagothrix* the gluteus maximus ends on the fascia lata. Klaatsch (1900) regards the muscle as stronger in *Alouatta* than in either *Ateles* or *Lagothrix*. The gluteus maximus of *Cebus* appears to be larger than in any of the other four prehensile-tailed cebids and always associated with a large caudofemoralis which, nevertheless, is not well separated from the large gluteus (Bodini, 1965). M. gluteus medius is large in *Ateles*, as could be expected from the broadened iliac blade of the animal. Waterman (1929) attributes this osteological character to the attachment on the pelvis of some muscles related to the brachiating habits of this genus. Its piriformis is intimately associated with the mesogluteus (Bodini, 1965; Hill, 1962). Roberta Bodini (personal communication) has informed me that this muscle, which she regards as just a part of the gluteus medius, is small in *Ateles* when compared to *Cebus*. To her this indicates that the rotating and abducting possibilities of the piriformis are reduced in the spider monkey. This situation is in general comparable to my findings in the howler where a small piriformis is closely associated to the larger gluteus medius. I was, nevertheless, able to identify and separate clearly the bellies of the two muscles. Their organization in *Brachyteles* (Hill, 1962) and *Lagothrix* (Bodini, 1965; Hill, 1962) practically duplicates the characters of the spider and howling monkey. The resemblance of *Brachyteles* to *Alouatta* is striking. Hill (1962) reports a cleavage plane through the medial gluteus very much like the one I described in the muscle of the howler. Bodini (1965) did not find a scansorius in *Ateles* and informs me that its gluteus minimus is very much reduced, otherwise these two muscles in *Lagothrix* (Bodini, 1965; Hill, 1962) and *Brachyteles* (Hill, 1962) resemble those of the howler. In *Cebus* the gluteus medius, pars piriformis, is strongly developed, contrasting with the pattern in the other four genera but resembling *Saimiri;* its gluteus minimus and scansorius have their origins occupying the entire supracetabular portion of the gluteal plane (Bodini, 1965).

Cruropedal Group

LATERAL DIVISION

M. peroneus longus: This long muscle covers the short peroneus and arises from (fig. 38) the lateral surface of the head and upper fifth of the fibular shaft, the peroneal portion of the crural aponeurosis and the fascia between the two peroneal muscles. Its fibers form a longitudinal belly (fig. 44), passing distally to the proximity of the

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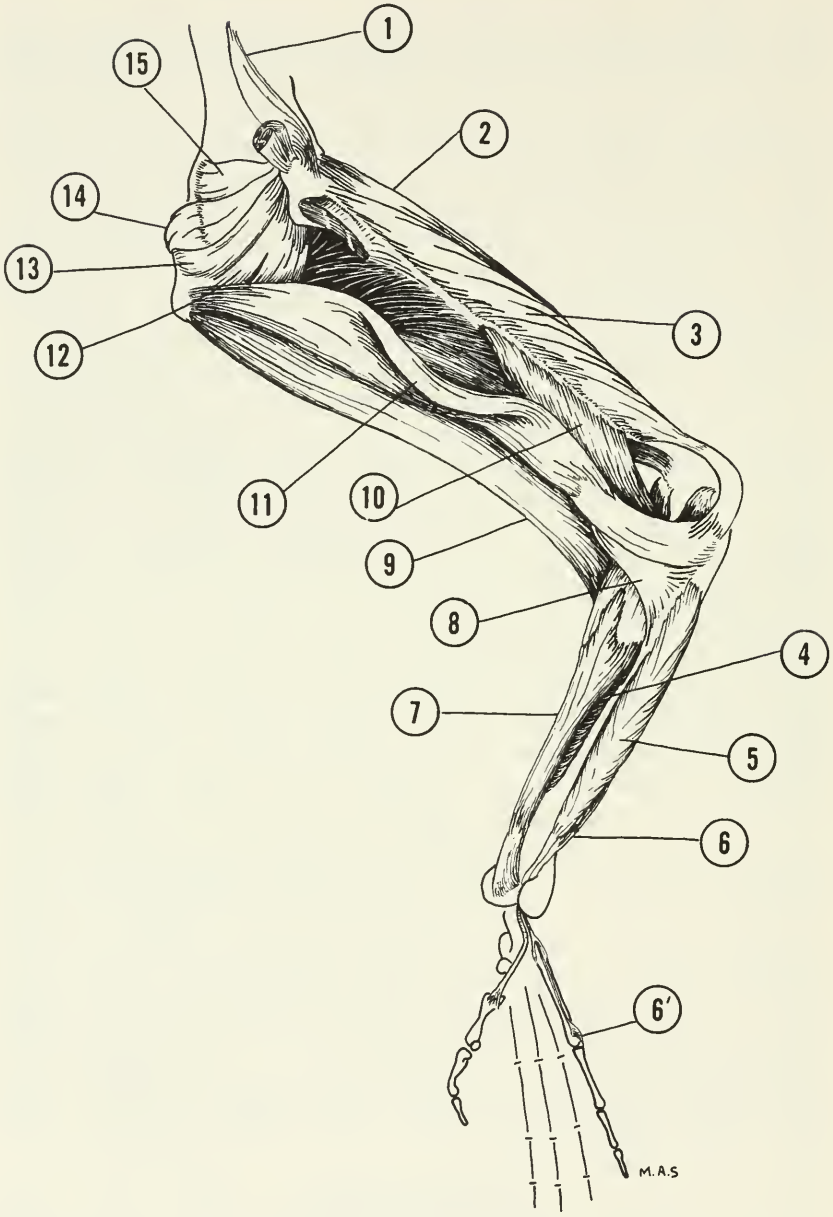

FIGURE 44.—Lower extremity (1, m. scansorius; 2, m. rectus femoris; 3, m. vastus lateralis; 4, m. soleus; 5, m. peroneus longus; 6, m. peroneus brevis; 6′, m. peroneus digiti quinti; 7, m. gastrocnemius; 8, trigonum subtendinosum; 9, m. semitendinosus; 10, m. biceps femoris, caput breve; 11, m. biceps femoris, caput longum; 12, m. quadratus femoris; 13, m. gemellus inferior; 14, m. obturatorius internus; 15, m. gemellus superior.

ankle where it changes into a round strong tendon. This enters the superior peroneal retinaculum superficial to that of the peroneus brevis, then passes over the lateral surface of the calcaneus, goes through the inferior peroneal retinaculum and leaves the brevis by approaching the plantar surface of the foot. The tendon here runs transversely across the cuboid and the plantar surface of the distal tarsal row where it is contained within an osteofibrous canal formed by the bones, the plantar ligaments of the foot and, particularly, on the tibial half, by the laterally diverging fibers of the tibialis posterior. Insertion takes place upon the lateroplantar side of the base of the first metatarsal. I found no difference between this muscle in the northern red howler and that of *Alouatta fusca* (Sirena, 1871) or *Mycetes niger* (=*Alouatta palliata*) studied by Frets (1911). The latter author's description is not complete.

Nerve supply: The common peroneal nerve sends a long branch to the lateral crural compartment which supplies all three muscles here included.

Function: Plantar flexion and eversion of the foot, opposition and flexion of the hallux.

M. peroneus brevis: It is the more anterior of the muscles in the lateral crural compartment. Origin is by fleshy fibers from the intermediate three-fifths of the lateral fibular surface (fig. 38), the upper fifth of the anterior intermuscular septum, and the fascia between this muscle and the longus. Near the superior peroneal retinaculum the elongated muscular belly gives rise to a round tendon which is now anterior to that of m. peroneus longus and grooves the rear aspect of the fibular malleolus. It curves around the distal end of this bone above and medial to the tendon of longus (fig. 44), runs along the lateral calcaneal surface between that tendon superficially and the one of the peroneus digiti V medially and enters its own compartment in the inferior peroneal retinaculum. The brevis tendon becomes superficial as the longus aims toward the plantar surface. The former is split by the tendon of m. peroneus digiti quinti into a fine deep and a larger superficial subtendon, both of which are inserted on the peroneal process of metatarsale V. The details of this muscle, as explained by Sirena (1871), accord with those of my study. The account of Frets (1911) is again incomplete.

Nerve supply: A branch of the common peroneal nerve.

Function: Plantar flexion and eversion of the foot.

M. peroneus digiti quinti: The third muscle of the lateral compartment of the leg lies between the other two peronei. Origin is from the distal fifth of the fibular shaft where the lateral surface of the bone twists backward to form the so-called peroneal canal (fig. 38) (see Testut and Latarjet, 1959) and from the septa which

separate this muscle from the other two peronei. Its belly narrows down to a small tendon which accompanies that of the peroneus brevis around the lateral malleolus, through the compartment for that muscle in the inferior peroneal retinaculum and then passes under the arch formed by the unequal splitting of the brevis tendon (fig. 44). The peroneus digiti quinti runs now superficially along the fibular side of the fifth metatarsal until it ends on the peroneal side of the dorsal extension expansion to this toe (fig. 45). The peroneus digiti quinti in *Alouatta fusca* (Sirena, 1871) is like that of the *seniculus* species. Its ending in *Mycetes niger* (=*Alouatta palliata*) is said (Frets, 1911) to be both on the peroneal process of toe V and the corresponding dorsal expansion. In my opinion, Frets (1911) overlooked the fact that the insertion on the fifth metatarsal belongs to m. peroneus brevis.

Nerve supply: A branch of the common peroneal nerve.

Function: Abductor of the fifth toe and the foot.

ANTERIOR DIVISION

M. tibialis anterior: It is the best developed of all three muscles in the anterior crural compartment. Fleshy fibers arise from (1) the upper half of the lateral tibial surface between the tibial crest and the weakly defined attachment of the interosseous membrane (fig. 38), (2) the tendinous septum which appears in the upper third of the leg between this muscle and the extensor digitorum longus, (3) the crural fascia, and (4) the interosseous membrane. Proximally, they reach the front of the lateral tibial condyle and distally, half way to the ankle, the elongated belly divides into two heads; one is continued over the lower third of the tibia as a smaller anterolateral and the other as a larger posteromedial round tendon. Both pass under the superior extensor retinaculum covering that of the extensor hallucis longus to reach the tibial border of the foot where they cross over the scaphoid and the medial cuneiform (fig. 45). The anterolateral tendon ends on the tibial side and plantar aspect of the base of metatarsale I. The posteromedial expands as it rolls over the cuneiform partially covered by the other portion of the tibialis anterior. Its insertion is on the plantar surface of that cuneiform and base of the first metatarsal. Other studies of this muscle in the howler monkey reveal no difference (see Sirena, 1871).

Nerve supply: The deep peroneal nerve.

Function: It produces dorsiflexion of the foot. By the anterolateral tendon it abducts the hallux and as a whole the muscle inverts the foot.

M. extensor hallucis longus: With origin from (1) a narrow area of the upper third of the interosseous membrane and (2) the septal

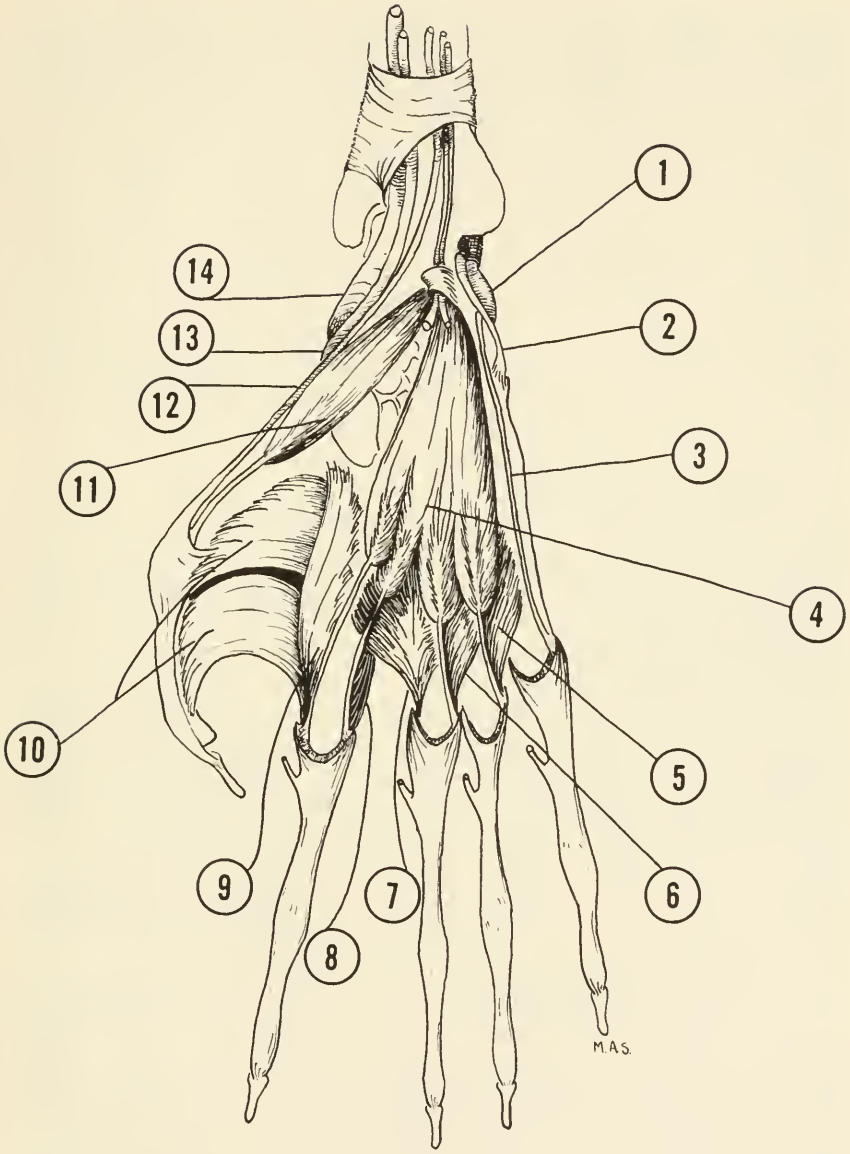

FIGURE 45.—Dorsal view of the foot (1, tendon of m. peroneus longus; 2, tendon of m. peroneus brevis; 3, tendon of m. peroneus digiti quinti; 4, m. extensor digitorum brevis; 5, fourth dorsal interosseus; 6, third dorsal interosseus; 7, second dorsal interosseus; 8, first palmar interosseus; 9, first dorsal interosseus; 10, m. adductor hallu is, caput obliquum et transversum; 11, m. extensor hallucis brevis; 12, tendon of m. extensor hallucis longus; 13, anterolateral tendon of m. tibialis anterior; 14, posteromedial tendon of m. tibialis anterior.

fascia between it and the other two muscles of the compartment, the extensor hallucis longus forms a fusiform belly between them and is covered by the extensor digitorum longus and tibialis anterior. It follows the latter into the superior extensor retinaculum where its fleshy fibers give rise to a long and narrow tendon which runs on the dorsum of the foot medial to the belly of m. extensor hallucis brevis (fig. 45). It now crosses superficially over the two tendons of the tibialis anterior before entering its own compartment of the inferior extensor retinaculum. On reaching the metatarsophalangeal joint of the hallux, the tendon sends dorsal tendinous expansions at each side toward the plantar aspect of the foot, the rest continues as a single tendon to be inserted on the dorsal base of the last hallucal phalanx. Sirena (1871) calls it *m. extensor hallucis proprius* and says it is as in man.

Nerve supply: A muscular ramus of n. peroneus profundus.

Function: It extends the two phalanges of the hallux.

M. extensor digitorum longus: This long muscle of the anterior crural compartment is bound medially by both the tibialis anterior and the extensor hallucis longus, laterally by the anterior intermuscular septum and the fibula. It arises from most of that septum, the crural fascia, and the intermediate two quarters of the medial fibular surface, very near the anterior margin of the bone, as most of this surface is taken up by the origins of the muscles in the posterior compartment of the leg. Additional fibers come from the interosseous membrane and in large number from the tendinous fascia which develops between the extensor digitorum longus and the tibialis anterior. The muscle runs distally on the lateral side of the latter, and the two almost completely cover the extensor hallucis longus. It changes into two strong tendons when approaching the superior extensor retinaculum under which they pass together with the other two members of the anterior division (fig. 45). The paired tendons cross the lateral and proximal part of the foot where they are held down by a powerful tendinous retinaculum. They now run toward the dorsum of the foot and expand as four flat bands united by fibrous tissue and contained within a division of the deep dorsal fascia which covers the bellies of the extensor digitorum brevis. Upon reaching the metatarsophalangeal joints of the last four toes each band sends an expansion along both sides of the corresponding articulation. These reach the transverse intermetatarsal ligaments with which they fuse and receive distally the insertions of the interossei and lumbricals. The rest of the band proceeds distally over the toe, intimately connected to the underlying interphalangeal capsules before ending on the dorsal base of the corresponding last phalanx. There are no differences with the muscle described by Sirena (1871) in *Alouatta fusca*.

Nerve supply: The muscle receives a branch from the deep peroneal nerve.

Function: It extends the two distal phalanges and according to Ströde (1937) contributes to spreading of the toes.

Pedal Group

M. extensor digitorum brevis et hallucis: Its origin is from the sinus tarsi where the anchorage of the retinaculum for the extensor digitorum longus divides it into a portion for the hallux and one for the other toes (fig. 45).

M. extensor digitorum brevis arises by fleshy fibers from the laterodorsal aspect of the greater calcaneal process. These group into four flat bipennate bellies which pass over the metatarsus deep to the tendons of the extensor digitorum longus. Each develops a central tendon which receives the insertion of the muscular fascicles. The tendons reach the metatarsophalangeal joints where the first two end by joining the deep aspect of both dorsal extensor expansions to the second toe, the first on the tibial side, the second on the fibular. The third and fourth tendons blend with the extensor expansion to the fibular side of the third and fourth metatarsophalangeal articulations.

M. extensor hallucis brevis originates from the dorsal surface of the greater calcaneal process where the insertion of the retinaculum already mentioned separates it from the bundles destined for the other toes. A flat belly is formed, larger than any of the previous part. A long tendon appears at its distal end, runs deep to that of the extensor hallucis longus and expands over the dorsum of the first metatarsophalangeal joint where it ends. Sirena (1871) does not report two tendons to the dorsal extensor expansion of the second metatarsophalangeal joint.

Nerve supply: The deep peroneal nerve.

Function: It extends the hallux and the next three toes at the metatarsophalangeal joints. It spreads toes II, III, and IV.

Comparative anatomy of the cruropedal and pedal groups.— The cruropedal muscles of *Ateles*, *Brachyteles*, and *Lagothrix*, all of which are covered to a certain extent by Hill (1962), can be easily matched to those of *Alouatta*. The findings of Ruge (1878a) in *Ateles* and *Cebus* also accord in general with my data on the howler. The extensor digitorum longus of the woolly monkey is said to supply tendons only for toes III, IV, and V (Hill, 1962). The two tendons of m. tibialis anterior in the woolly spider monkey are inserted, respectively, on the navicular and on the base of metatarsale I (Hill, 1962). This animal has only three bellies destined for toes II, III, and IV from the extensor digitorum brevis and its m. peroneus digiti quinti is described by Hill (1962) as just a small tendon given off from that

of the peroneus brevis in the tarsus and going to the head of the metatarsal.

Ventral Musculature

Coxofemoral Group

PREPELVIC

M. pectineus: This is a triangular muscle which, arising by fleshy fibers from the iliopectineal line (fig. 36) in front of the insertion of the external oblique, passes distally into the thigh, forming the medial side of the floor of the femoral triangle. The pectineus is inserted on the upper fourth of the medial lip of the linea aspera in front of m. adductor longus (fig. 40) and is divided into a medial and lateral half by the nerve to the gracilis. Both parts are very thin near their attachment. Sirena (1871) says that this ending takes place by a tendon. This contrasts with my observations of a thin muscular insertion upon the femur.

Nerve supply: The lateral portion is innervated by a branch of the femoral nerve which, after passing deep to the femoral vessels, reaches the muscle on its deep surface. The medial receives a branch from the anterior ramus of the obturator nerve.

Function: Adduction and lateral rotation of the femur.

M. obturatorius externus: This muscle is deep to all those found in the angle between the femur and the innominate bone. It arises by fleshy fibers from most of the ventral three-fourths of the obturator foramen (fig. 36). This includes the borders of the opening formed by the body of the pubis, its two rami, and the lower ischial ramus. Many of the fascicles have origin on the obturator membrane. The bundles of the external obturator are directed dorsally to form a flattened tendon which glides over the femoral surface of the ischium, passes below and then behind the anatomical neck of the femur to insertion in the rear of the trochanteric fossa (fig. 40). The muscle is pierced by the posterior ramus of the obturator nerve. Sirena (1871) points out that it is better developed than in man.

Nerve supply: The posterior ramus of the obturator nerve.

Function: Lateral rotation of the femur.

M. adductor longus: This is the most ventrally placed of all three adductor muscles and lies in front of the brevis and magnus but behind the pectineus. The adductor longus arises by muscular fibers from (1) the iliopectineal line near the symphysis, (2) the femoral surface of the pubic body and part of its lower ramus. This origin lies between those of gracilis superficially and the external obturator deeply (fig. 36). The muscle is composed of thick and fleshy bundles connected by areolar tissue and easy to separate. Its fibers run disto-

medially between the pectineus and adductor brevis, forming a broad triangular partition which is inserted by fleshy fibers on the medial lip of the linea aspera, from the beginning of the medial supracondylar line to the proximity of the lesser trochanter (fig. 40). The muscle is very thin near its femoral insertion. The adductor longus is separated from the vastus medialis in front by the thin pectineus, and from the ischiofemoral part of the adductor magnus behind by the previs. The medial circumflex vessels cross the upper border of the long adductor as they pass to the posterior muscular compartment of the thigh and separate this border from the external obturator. Sirena (1871) found on the right side of one of his specimens that the adductor longus was one-third narrower than the muscle in the left.

Nerve supply: The anterior ramus of the obturator nerve.

Function: Adduction of the thigh.

M. adductor brevis: This is actually larger than the adductor longus between which muscle and the adductor magnus it lies. The brevis arises from the lower ramus of the pubis on its femoral surface between the other two adductor muscles (fig. 36). This origin extended up into the body of the pubis in the female. The muscle forms an anteroposteriorly compressed septum similar in appearance to that of the longus and passes distomedially to be inserted on the linea aspera for a longer distance than that muscle (fig. 40). Its upper border is in close relation to the lower one of the quadratus femoris.

Nerve supply: The posterior branch of the obturator nerve pierces the membrane and the external obturator to reach the adductor brevis ventrally and near its upper border. It supplies the muscle and continues its path through the belly to innervate the ischiofemoral part of the adductor magnus.

Function: Adductor of the thigh.

M. adductor magnus: The larger of the adductor muscles is easily differentiated into two parts, the ischiofemoralis and the ischiocondyloideus. The origin of the magnus is by tendinous and fleshy fibers from the femoral surface of the lower ramus of the ischium between the semitendinosus dorsally and the adductor brevis ventrally (fig. 36). The magnus covers the beginning of the semimembranosus, with which it is closely associated, and also that of the quadratus femoris. Immediately after the origin, the muscle is divided into its two parts which may remain narrowly apposed to each other for a long distance.

Pars ischiofemoralis is found as a large anteroposteriorly compressed triangular muscular body between the adductor brevis and the ischiocondyloideus. Its fibers form muscular bundles that can be easily separated. They run toward the femur and are inserted all along the linea aspera from the medial supracondyloid line to ap-

proximately 1 cm below the higher point of the adductor brevis (fig. 40).

Pars ischiocondyloideus should be treated with the postpelvic group, but I include it here for topographical reasons. Its fibers of origin are more superficial than those of the ischiofemoralis and have a more direct association with the tendon of the semimembranosus. It descends along the medial side of the thigh and reaches the junction of the medial epicondyle with the medial supracondylar line, where it is inserted (fig. 40). Some of its fibers are attached to the medial head of the gastrocnemius. Sirena (1871) regards the ischiofemoralis only as adductor magnus and calls the ischiocondyloideus m. adductor quartus.

Nerve supply: The ischiofemoralis is supplied by the continuation of the posterior ramus n. obturatorius and the ischiocondyloideus by the same branch of the n. tibialis that innervates the hamstring muscles.

Function: Adductor of the thigh.

M. gracilis: This band-shaped muscle is the most superficial of those on the medial side of the thigh. The gracilis, broader near origin than at insertion, arises by strong fleshy fibers from (1) the public crest in front of the insertion of the abdominal muscles, (2) the femoral surface of the body of the pubis at the side of the symphysis, and (3) a short stretch of the lower pubic ramus on its distal border (fig. 36). A wide and flat belly is thus formed which descends along the medial side of the thigh, covering the pectineus and the three adductors. Midway between its origin and insertion, the gracilis has narrowed considerably from its initial wide proportions. The muscle passes dorsomedial to the knee where it is covered by the sartorius, with the saphenous nerve and vessels intervening. Beyond this point the gracilis is bound within a narrow aponeurotic compartment with the underlying semitendinosus. It ends by fanning out into two orders of fibers, which, nevertheless, form a single continuous sheet of insertion. The proximal part is aponeurotic and the distal muscular (fig. 37). This mixed attachment takes place behind that of the sartorius, with the muscular part reaching further down along the tibia than the sartorial fascicles (fig. 38). Sirena (1871) describes this insertion as being common with that of the semitendinosus on the anterior tibial crest and adds that the fasciae of these two muscles fuse distally and descend down to the medial malleolus of the ankle.

Nerve supply: The anterior branch of the obturator nerve sends a large branch to the gracilis through the pectineus.

Function: Flexor of the knee and adductor of the thigh.

Comparative anatomy of the prepelvic coxofemoral group.—This group of muscles in *Ateles*, *Brachyteles*, and *Lagothrix* has a strong

resemblance to those of the howling monkey. There is in all of them a division of the pectineus into two portions which are supplied by the femoral and the obturator nerve, respectively, and the separation of the adductors is not very clear (Hill, 1962). According to Bodini (1965), the pectineus is not divided in *Ateles*, and her observations of the adductors in this genus reveal these muscles as almost impossible to individualize. The resemblances of these animals to the howler in reference to this group of muscles apply also to *Cebus*. Bodini (1965), however, did not find an adductor brevis in the two specimens of capuchin she studied.

POSTPELVIC

The observations of other authors (Bodini, 1965; Hill, 1962; Sirena, 1871; Waterman, 1929) on the ventral postpelvic muscles of *Alouatta* do not call for any special comments.

M. obturatorius internus: Forming the outer wall of the ischiorectal fossa, its origin is from (1) the inner surface of the upper arm of the pubis up to the iliopubic junction, (2) the body of the pubis, (3) the ischiopubic bar, and (4) the obturator membrane. Its fibers converge toward the upper ramus of the ischium where they form a tendon which sometimes is divided into two. This passes over the rudimentary lesser sciatic notch and into the deep part of the gluteal region. After crossing behind the neck of the femur, the tendon ends on the trochanteric fossa (figs. 40, 41).

Nerve supply: The pudendal nerve sends a branch to the muscle in the pudendal canal.

M. gemellus superior: This is a small and somewhat rectangular belly composed of thick fleshy bundles arising from the femoral side of the sciatic spine and the upper part of the lesser sciatic notch (fig. 36). It crosses over the iliofemoral articular capsule to end at the bottom of the trochanteric fossa together with the tendinous fibers of the internal obturator and the other gemellus (fig. 40). The tendon of the extrapelvic portion of that muscle is applied against the posterior border of the gemellus, which is here grooved to lodge that tendon. The muscle is perforated by its nerve which continues distally deep to the internal obturator to supply the other gemellus and the quadratus femoris.

Nerve supply: The nerve to the two gemelli and the quadratus femoris (fig. 35).

M. gemellus inferior: It is of similar shape as its homonym and of approximately equal size. The gemellus inferior is found between the extrapelvic portion of the obturator internus and the upper border of the quadratus femoris. It arises by fleshy fibers from the femoral surface of the body of the ischium near the tuberosity and adjacent border of the lesser sciatic notch (figs. 36, 41). These fibers

form thick muscular bundles which pass behind the iliofemoral articular capsule and are inserted at the bottom of the trochanteric fossa (fig. 40).

Nerve supply: It is supplied by the same nerve as the gemellus superior.

M. quadratus femoris: This muscle, about twice as large as either of the two gemelli, is found deep in the limit between the gluteal and dorsal regions of the thigh (fig. 44). It arises by fleshy fibers from the femoral surface of the ischial body deep to the common origin of the biceps and semitendinosus (fig. 36). The quadratus femoris passes laterally covering the trochanter minor and is inserted by fleshy fibers over a triangular area of the proximal part of the femoral shaft bound by the lesser trochanter, the intertrochanteric crest, and the insertion of m. gluteus maximus on the outer line of the linea aspera (fig. 40). It is entirely covered by the long head of the biceps which is here associated with the semitendinosus as these two muscles leave the ischial tuberosity on their way to the back of the leg. The sciatic trunk and its long branch for the hamstring muscles pass distally between the biceps and semitendinosus superficially and the quadratus femoris on a deeper plane. The caudal border of the muscle is related to the upper border of the adductor brevis.

Nerve supply: It is innervated by the continuation of the same nerve which supplies the two gemelli.

Function: These four muscles are lateral rotators and abductors of the femur.

M. biceps femoris: This muscle has a long and a short head. The second belongs, on the basis of its innervation, with the postpelvic group of the dorsal muscles supplied by the n. peroneus communis, but I consider it here for topographical reasons. The robust caput longum is found on the superficial and lateral aspect of the dorsum of the thigh extending between ischium and tibia (fig. 44). The caput breve lies below the middle of the thigh under cover of the long component of the muscle (fig. 44). The caput longum arises in common with the semitendinosus by a large fleshy mass whose fibers are fixed to the femoral surface of the ischial body behind the origin of the quadratus femoris and the complex of the ischiocondyloideus and semimembranosus (fig. 36). The sciatic trunk and the nerve supply of the hamstring muscles separate this head from the underlying structures. A little beyond the middle of the thigh the fibers of the biceps form a transversely flat tendon which expands as it approaches the leg by passing behind the knee when this is in the normal flexed position of the limb. This tendon is inserted on the anterior aspect of the lateral tibial condyle (figs. 38, 39) after gliding over the head of the fibula.

The caput breve has a double origin: (1) Its proximal fibers arise from the dorsum of the lateral intermuscular septum below the middle of the thigh. This membranous origin was described by Klaatsch (1900) as taking place from the gluteal fascia. (2) As we approach the knee the short bicipital fascicles come from the lateral supracondylar line down almost to the corresponding condyle (fig. 40). Most fibers of septal origin soon join the deep aspect of the long biceps and, as pointed out by Klaatsch (1900), their respective fibers are to be differentiated more by their direction than by a real division between one caput and the other. The rest of the short bundles run distally, deep to the longus tendon, to end by blending with the crural aponeurosis over the proximal fourth of the leg, where its thin fibers form a weak trigonum subtendinosum (fig. 39).

Nerve supply: The short head receives a branch from the peroneal nerve low down in the popliteal region. The long head is supplied by a ramus of the tibialis nerve which also innervates the other postpelvic ventral muscles of the thigh.

Function: The caput longum is an extensor of the hip and a flexor of the knee, where it also acts as a lateral rotator. The caput breve flexes the knee.

M. semitendinosus: The long semitendinosus extends from the ischium to the medial side of the knee and the tibia. It has a common origin with the caput longum biceps femoris from the lateral surface of the ischial body (fig. 36). A muscular mass arises here on the rear part of the distal border and after a short distance the two muscles separate, the semitendinosus following a distomediad direction covers the semimembranosus and forming the medial margin of the popliteal space (fig. 44). On reaching the medial side of the knee, it is contained together with m. gracilis within a common aponeurotic compartment; it then expands and is inserted on the medial surface of the tibia as the deepest muscle of the pes anserinus (figs. 37, 38).

Nerve supply: N. tibialis.

M. semimembranosus: This muscle extends from the ischium to the medial side of the knee joint. Origin is by tendinous fibers on the femoral surface of the lower ischial ramus deep to the fascicles of the ischiocondyloideus (fig. 36). The semimembranosus descends under cover of the semitendinosus and passes behind the medial epicondyle of the femur to be inserted by a robust, short, and flat tendon on the medial tibial condyle under cover of the medial ligament of the knee joint (figs. 37, 38). Some of its fibers pass toward the axis of the femur at a right angle to the back of the articular capsule, with which they are fused.

Nerve supply: N. tibialis.

Function: These two muscles are extensors of the hip and flexors of the knee.

Comparative anatomy of the postpelvic coxofemoral group.—*Alouatta* shares with *Ateles* (Bodini, 1965; Hill, 1962; Klaatsch, 1900), *Brachyteles* (Hill, 1962) and *Lagothrix* (Bodini, 1965; Hill, 1962; Klaatsch, 1900) a bicipital biceps femoris and thus contrasts with *Cebus*, in which the biceps has no short head but, on the other hand, possesses a m. tenuissimus (Bodini, 1965; Klaatsch, 1900). Klaatsch (1900) regards this muscle as homologue to the caput breve of the biceps. Bodini (1965) agrees with Sirena (1871) that the hamstring muscles of the howler are strong flexors of the knee and, I add, also extensors of the thigh. From Bodini's work, which is still in progress (personal communication), I get the impression that these extensors of the thigh are more developed in *Alouatta* than, at least, in the spider monkey. This would indicate that the extension of this part of the hind limb and the flexion of the knee in the howler are functionally more important than in *Ateles*.

Cruropedal Group

M. gastrocnemius: This two-bellied muscle extends between the distal end of the femur and the calcaneus (fig. 44). A caput laterale originates by tendinous fibers from the lateral epicondyle on a well-marked impression found in this part of the bone above the popliteal groove (fig. 40). Additional tendinous and fleshy elements come from the portion of the articular capsule covering the back of the lateral femoral condyle. The tendinous fibers spread out as a shiny aponeurotic lamina in the upper fifth of the lateral half of this head. This belly joins those of the other head and of the soleus to form a common tendon whose attachment is on the posterior end of the calcaneus. A caput mediale arises by tendinous fibers from the medial epicondyle right below the attachment of m. adductor magnus (fig. 40), and more laterally by fleshy fibers from the articular capsule covering the medial femoral epicondyle. The tendinous elements expand over the dorsal surface of the muscle for a longer distance than in the opposite head. Insertion takes place on the calcaneus as described before. A sesamoid develops within the tendinous origin of each belly from each epicondyle. The two bellies are closely apposed along the axis of the limb, but it is only beyond the intermediate level of the crus that they fuse to form a single muscle whose fleshy fascicles extend as far as the heel. The sural nerve passes between the two heads at the distal angle of the popliteal space. The short saphenous vein, collecting blood from as far as the dorsum of the foot, enters the space at this same point and empties into the popliteal vein. The posterior tibial nerve passes distally deep to the medial head and after m. soleus has joined the gastrocnemius it runs under cover of the medial border of the combined muscle. The gastrocnemius in *Alouatta fusca* (Sirena, 1871) offers no difference.

Nerve supply: The tibial nerve gives a branch to each head in the popliteal space.

Function: Flexion of the knee and plantar flexion of the foot.

M. soleus: This other muscle of the superficial dorsal crural compartment arises from the posterior slope of the head of the fibula by strong tendinous fibers (fig. 38). They give rise to the fleshy bundles while expanding on the deep and proximal part of the belly. The soleus appears now as a dorsoventrally flattened structure which joins the overlying gastrocnemius in the intermediate third of the crus (fig. 44). A long tendon of Achilles is formed within the combined muscle and is covered by fleshy fibers on its two surfaces all the way down to the calcaneal tuberosity, from which it is separated by a large bursa. Its insertion is on the plantar surface of the tuberosity. Sirena (1871) explains that a delicate aponeurotic lamina develops on the deep aspect of the triceps cruralis and attaches to the upper and lateral margins of the tuberosity. The bursa thus forms between this sheet and the main tendon.

Nerve supply: N. tibialis.

Function: Plantar flexion.

M. popliteus: Origin is by an intracapsular round tendon from the lateral epicondyle in front of the beginning of the lateral head of gastrocnemius (fig. 40). It travels posteriorly in a groove marked between the articular surface of the lateral condyle and the lateral origin of the gastrocnemius. The tendon enters the dorsal compartment of the leg by piercing the capsule. The fleshy fibers of the muscle are now directed medially under the soleus and gastrocnemius, the proximal ones quite horizontally and the distal with a sharp inclination toward the tibia. They form a large triangular mass before being inserted on the posterior surface of this bone from the posterior border of the medial epicondyle to the popliteal line (fig. 38). Along the medial margin of the tibia the fibers of the muscle attach to the medial intermuscular septum. Sirena (1871) describes the origin a little bit differently but essentially the same from the lateral epicondyle. He notes the large size of the muscle.

Nerve supply: A fine branch of the tibial nerve.

Function: It flexes the knee and produces some rotation of the leg on the joint to the extent that the ligaments allow this displacement.

M. flexor digitorum fibularis: It is the largest of the muscles in the deep dorsal crural compartment (fig. 46). The long belly arises (fig. 38) by fleshy fibers from (1) almost the entire dorsal and medial surface of the fibula, (2) by initially tendinous fascicles from the head of the fibula in common with the soleus, (3) the lateral half of the lower two-thirds of the interosseal membrane, and (4) the transverse intermuscular septum. These fleshy bundles descend to the ankle,

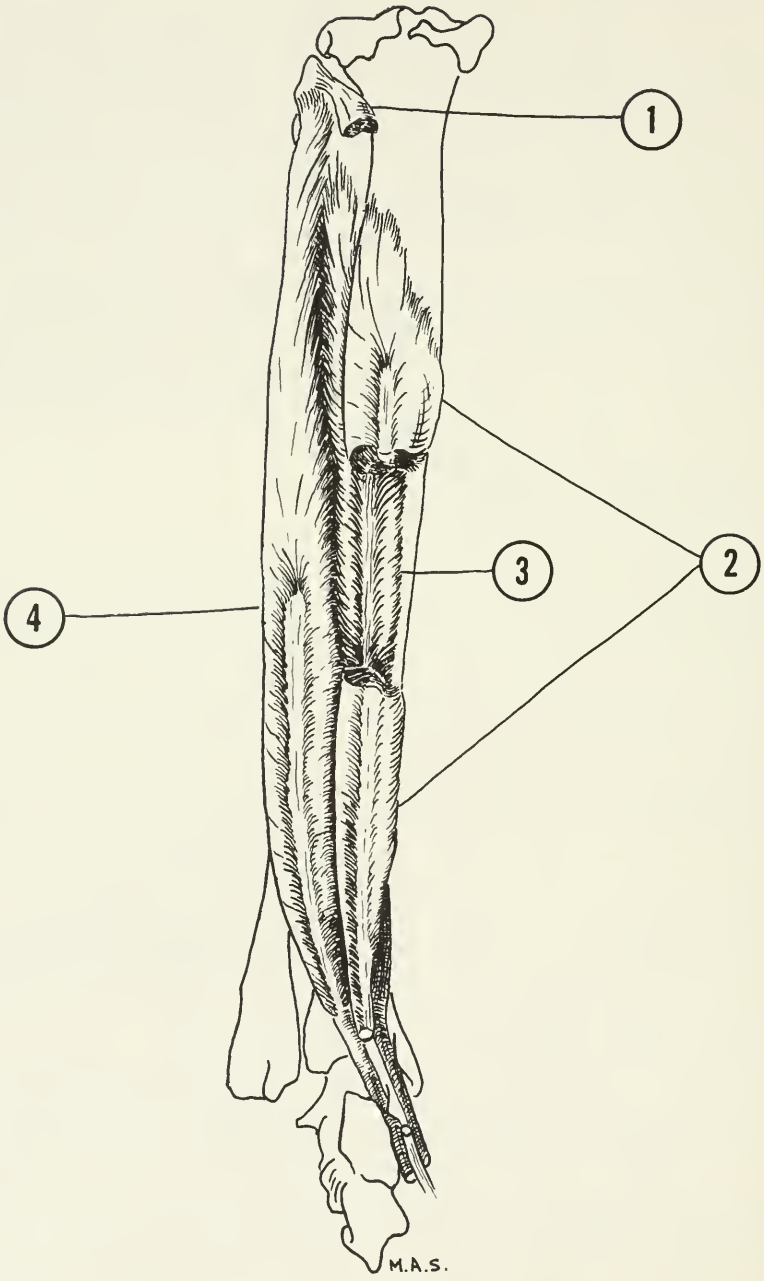

FIGURE 46.—Muscles of the deep dorsal crural compartment (1, m. soleus; 2, m. flexor digitorum tibialis, sectioned; 3, m. tibialis posterior; 4, m. flexor digitorum fibularis).

ending on the deep aspect of a long tendon which develops on the dorsum of the muscle at about the middle of the leg. The tendon glides over a groove of the posterior end of the talus transformed into an osteofibrous canal by the tendinous fibers which join its two edges. It is the deepest structure in the so-called medial calcaneal canal (see Testut and Latarjet, 1959) and reaches the central plantar compartment, where it is covered by that of the flexor tibialis (fig. 47). Its fibers form the powerful tendon to the hallux and the perforating tendons to toes II to IV in combination with contributions from the tibial flexor. The distal part of each of these tendons is inserted on the plantar base of the respective distal phalanx. Sirena (1871) refers to this muscle as flexor hallucis and says that it contributes only to the tendons of the hallux, third, and fourth toes.

Nerve supply: A muscular ramus of the tibial nerve.

Function: It contributes to the flexion of the distal interphalangeal joint in toes I to IV, its influence decreasing from the first to the fourth.

M. flexor digitorum tibialis: Origin (fig. 38) is by fleshy fibers from (1) the lower lip of the long popliteal line, (2) the intermediate three-fifths of the dorsal tibial surface along a narrow area bound medially by the popliteal line and the attachment of the transverse septum on the medial margin of the tibia and laterally by the origin of m. tibialis posterior, and (3) the septum between the two tibial flexor muscles. A long muscular belly is formed, the fibers of which extend through the ankle into the foot where they seem to be continued by those of the deep head m. flexor brevis without any interruption (fig. 7). Their insertion is on a long tendon which develops in the muscle midway between the knee and the foot. In the tibial retinaculum it is superficial to that of m. tibialis posterior (fig. 47) and is accompanied by the tibial nerve and the posterior tibial vessels. In the medial calcaneal canal (see Testut and Latarjet, 1959) it passes directly under and against the sustentaculum tali until in the central compartment it joins the tendon of the deeper lying flexor fibularis. Its fibers form the long perforating tendon to the fifth and contribute to the tendon of the other toes (fig. 47). Only a few fascicles join the tendon of the flexor fibularis to the hallux. The description of this muscle by Sirena (1871) is not very clear, but it appears as if he found the same arrangement as I did.

Nerve supply: A muscular ramus of the tibial nerve.

Function: It flexes the distal phalanx of toe V and contributes to the same function in the remaining pedal digits.

M. tibialis posterior: It lies completely covered by the flexor tibialis (fig. 46) and arises (fig. 38) by fleshy fibers from (1) the dorsal tibial surface laterally to the origin of the former muscle,

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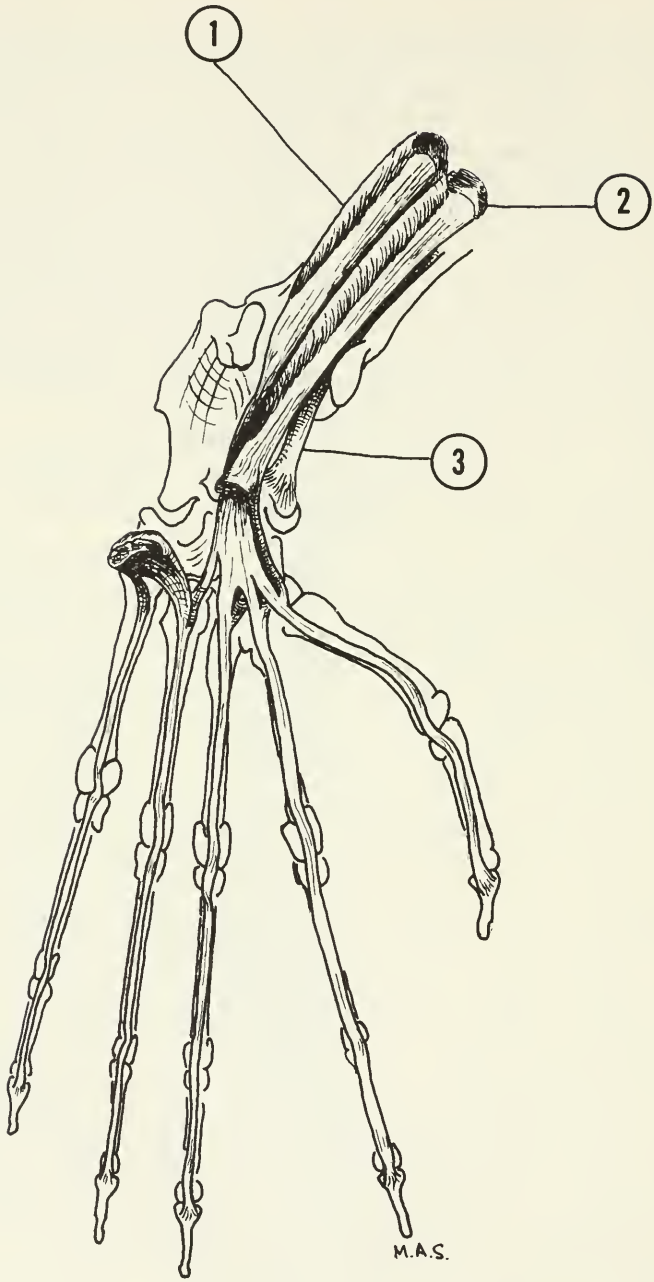


FIGURE 47.—Plantar view of the left foot and ankle (1, m. flexor digitorum fibularis; 2, m. flexor digitorum tibialis; 3, m. tibialis posterior).

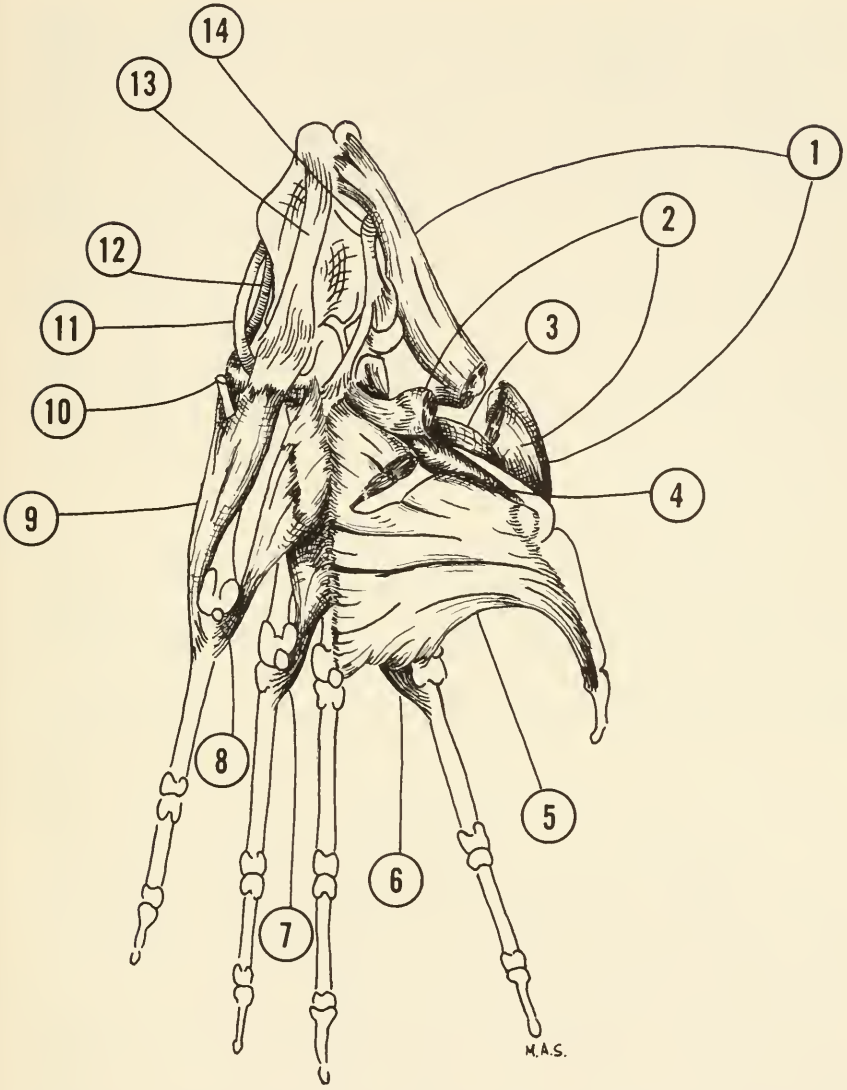


FIGURE 48.—Plantar view of the foot (1, m. abductor hallucis; 2, m. flexor hallucis, caput tibiale; 3, m. opponens hallucis; 4, m. flexor hallucis, caput fibularis; 5, m. adductor hallucis (contrahens I); 6, m. contrahens II; 7, m. contrahens IV; 8, m. contrahens V; 9, m. flexor digiti quinti; 10, tendon of m. abductor digiti quinti (=abductor digiti minimi of N.A.); 11, tendon of m. peroneus longus; 12, tendon of m. peroneus brevis; 13, lig. plantare longum; 14, tendon of m. tibialis posterior).

(2) the entire dorsal aspect of the interosseous membrane in the upper third of the leg, the area of its membranous origin diminishing distally to a narrow strip along the tibia, and (3) the septum between the two tibial flexors. The belly descends to the proximities of the ankle and its fibers are attached to the anterior aspect of a long tendon which forms within the muscle very high up in the leg. As it approaches the distal end of the tibia, the tendon changes from deep to medial in relation to the flexor tibialis (fig. 47). It passes around the lower end of the bone in a groove on the dorsal border of the tibial malleolus. After running through the tibial retinaculum, this tendon enters the medial calcaneal canal (see Testut and Latarjet, 1959) before ending on the plantar surface of the navicular (fig. 48), where it expands in taking firm insertion. Some of its fibers pass distolaterally underneath the calcaneonavicular ligament before ending in the middle of the tarsus upon the third cuneiform. Sirena (1871) adds a peroneal origin.

Nerve supply: N. tibialis.

Function: Plantar flexion and some inversion of the foot.

M. quadratus plantae: A rectangular flattened muscle arising deep to the origin of the flexor digitorum brevis, caput superficiale, from the medial aspect of the calcaneal tubercle. Its fleshy belly runs distally along the fibular border of the flexor tibialis and over the plantar aspect of the flexor fibularis. Insertion is in the distal part of the tarsus on the fibular border of the flexor tibialis. The lateral plantar nerve crosses the plantar surface of the muscle after passing between the two parts of the flexor digitorum brevis. Sirena (1871) found the muscle in all his specimens and notes that it is better developed than in man. Ströde (1937) also reports it in his howler.

Nerve supply: A small branch of the lateral plantar nerve reaches the muscle near its origin and also sends a twig to the ankle joint.

Function: By pulling on the still undivided tendon of the flexor tibialis it enhances the action of the long flexor upon the toes.

Comparative anatomy of the cruropedal group.—The differences between *Alouatta* and *Ateles* (Glaesmer, 1910; Hill, 1962), *Brachyteles* (Hill, 1962), and *Lagothrix* (Hill, 1962) in the cruropedal group of the ventral musculature appear to be of no major significance. Frey (1913) studied the triceps surae of the Primates in great detail and found that in *Cebus* the gastrocnemius tends to arise more from the knee capsule than from the back of the femur. Contrariwise, in *Ateles* more fibers come directly from the bone, as was the case with my howlers. Frey (1913) describes sesamoids at the origin of each head of the gastrocnemius in both the capuchin and the spider monkey, Glaesmer (1910) does not say anything about their presence or absence in either genus, and Hill (1962)

asserts that they do not exist in *Brachyteles*. Only Glaesmer (1910) attributes an origin to the soleus in *Ateles variegatus* (=*Ateles belzebuth*) from the upper third of the fibula. In this animal the distribution of tendons of the flexor tibialis and peroneus seems to differ from what Straus (1949) has indicated to be a typical platyrrhine pattern and which I have confirmed in the howler. Its flexor fibularis, together with the tibialis, forms the long tendon to toes I, II, and IV, and supplies all of that for the third; the tibialis contributes to the perforating tendons of toes I, II, and IV, and supplies the whole of that to V (Glaesmer, 1910). In *Ateles ater* (=*Ateles paniscus*) the tibialis forms the tendon to V and contributes to that of the fourth together with the flexor fibularis which also supplies tendons for toes I, II, and III (Glaesmer, 1910). The flexor tibialis of *Cebus "monachus"* provides the tendon to V and with the fibularis contributes to that of the hallux. The other toes receive their long tendons from the peroneal flexor (Glaesmer, 1910). The flexor fibularis and the tibialis of the woolly spider monkey (Hill, 1962) also depart from Straus' pattern (see Straus, 1949). In this animal the first supplies the tendon to the hallux together with a contribution from the fibularis. In addition, it forms the long tendons to toes IV and V. The fibularis, on the other hand, is responsible for those to the II and III. All the authors concerned agree on the presence of a plantaris only in *Cebus* and of m. quadratus plantae in all the genera.

Pedal Group

SUPERFICIAL SERIES, SUPERFICIAL LAYER

M. abductor hallucis: This powerful and long muscle arises by fleshy fibers from the medially projecting calcaneal tubercle (there is no lateral tubercle) and from the outer surface of the tibial flexor retinaculum as this passes toward the tibial malleolus (fig. 48). The belly thus formed runs distally along the medial canal of the calcaneus, where it covers the tendons, vessels, and nerves which enter the foot from the dorsum of the leg. The tibial edge of the plantar aponeurosis provides for the origin of more fleshy fibers. An additional group of tendinous elements reaches the peroneal side of the muscle at the level of the naviculocuneiform joint. These fibers have a common origin with those of the flexor hallucis brevis, caput tibialis, from the plantar aspect of the second cuneiform. Insertion takes place over a long tendon which begins in the center of the muscle opposite the first cuneiform. The tendon is separated from the first metatarsal by the tibial head of m. flexor hallucis brevis. Final insertion is on the tibial base of the first hallucal phalanx after establishing a firm connection with the underlying metatarsophalangeal joint capsule.

Nerve supply: The medial plantar nerve sends a branch to the muscle while in the calcaneal canal.

Function: Abduction of the first toe.

M. flexor digitorum brevis: The perforated flexor lies deep to the plantar aponeurosis in the central foot compartment, where it covers the two long flexor tendons.

The caput superficiale is well developed and forms a flat, distally tapering belly whose fleshy fibers arise from the calcaneal tubercle. In the female some fascicles come from the proximal part of the plantar aponeurosis. The origin is covered by that of m. abductor hallucis. In the middle of the metatarsus the head gives rise to two (one male, fig. 49d) or three tendons (two males, fig. 49a, b; one female, fig. 49c).

The caput profundum is separated from the superficialis by the lateral plantar nerve and accompanying vessels. Its fleshy fibers arise from the plantar surface of the flexor tibialis tendon and by a few distal slips from that of the fibularis. They are continuous without interruption with the muscular fibers of the tibial flexor as described above. This head divides into four bellies from which individual tendons proceed toward the second to fifth toes (two males, fig. 49b, d; one female, fig. 49c), except in one male (fig. 49a), where only two bellies are formed. These supply the perforated tendons to toes III and IV, that for the fifth coming as a direct branch of the long flexor tendon to toe V. Typically, a perforated tendon splits distal to the base of the first phalanx, the two resulting fascicles inserting on the margins of the corresponding second phalanx. They are joined by vincula brevia to that bone.

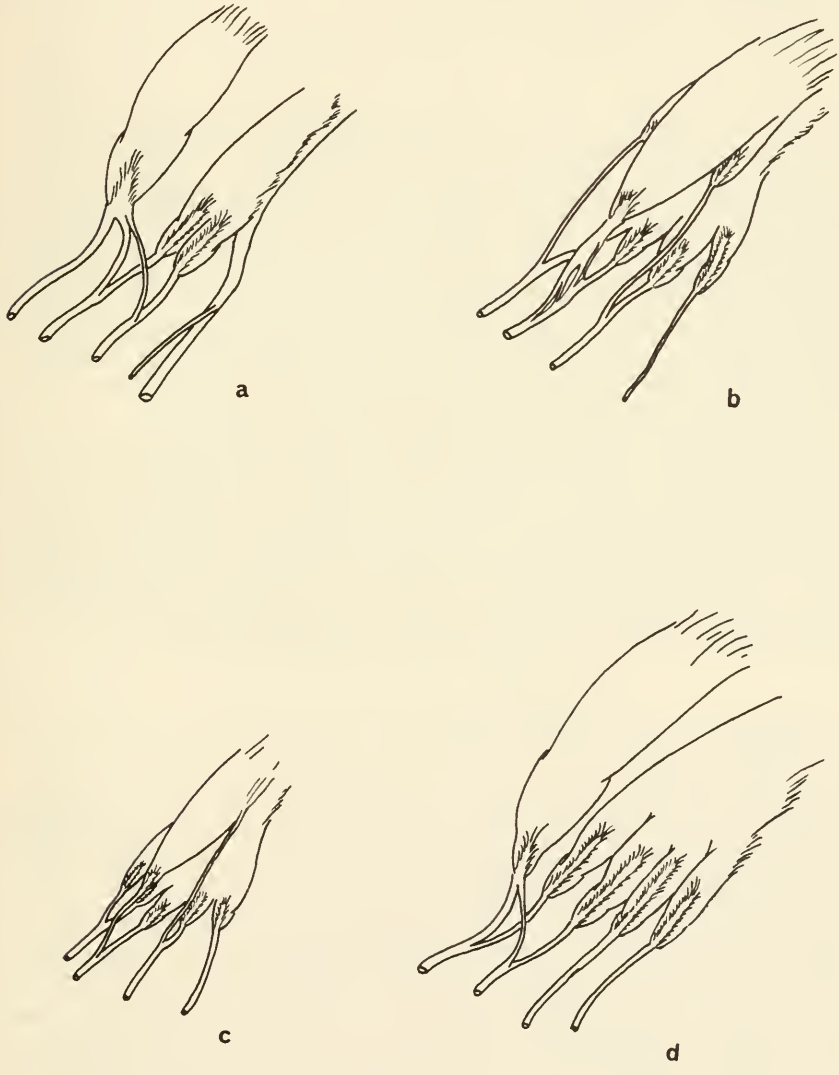
The pattern of the muscle in *Alouatta fusca* (Sirena 1871) differs from any of those described here. In this species the caput superficiale forms the short tendons to toes II and III, the profundum those for the fourth and fifth plus a contribution to the tendon of the third. Sawalischin (1911) found the superficial head of a *Mycetes* (=*Alouatta* giving a small tendon to toe II and a large one to III; the deep head provided a more robust contribution to the tendon of II, a fine one to that of III, and the single tendons for IV and V. Hill's (1962) description of the muscle resembles that of Sawalischin, except that the third toe tendon received no apparent contribution from the deep head.

Nerve supply: A branch of the medial plantar nerve enters the superficial head on its plantar aspect in approximately the middle of the belly, supplies it, and then innervates the deep one.

Function: Flexion of the toes at the proximal interphalangeal joints.

M. abductor digiti quinti (=*abductor digiti minimi of N.A.*): This muscle is not as well developed as the abductor of the hallux and was

absent in the left side of one male. It lies along the peroneal half of the plantar surface of the tarsus. Origin is by a mixture of fleshy and tendinous fibers from the lateral side of the calcaneal tubercle. Its compressed belly receives additional fibers from the plantar aponeurosis. The medial border of the muscle is next to the caput superficialis of the short digital flexor. It covers the quadratus plantae. As the abductor approaches the tarsometatarsal joint of the fifth toe, it splits into two tendons. One tendon, which is short, round, and



M.A.S.

FIGURE 49.—Distribution of tendons of m. flexor digitorum brevis.

stout, is attached to the peroneal process of metatarsale V together with m. peroneus brevis (m. abductor ossis metatarsi V), the other tendon, less powerful but long, crosses the fifth metatarsophalangeal articulation, pierces the flexor digiti quinti and ends on the fibular base of the first phalanx of toe V. Sirena (1871) found it to be a slender muscle on whose tendon many fibers of the flexor digiti quinti ended. He did not describe an abductor ossis metatarsi V.

Nerve supply: Lateral plantar nerve.

Function: Abducts the fifth toe.

SUPERFICIAL SERIES, DEEP LAYER

Mm. lumbricales: They are four round, small, but long muscles. The first originates from the tibial side of the perforating tendon to toe II the second, third, and fourth lumbricals arise from the adjacent sides of the perforating tendons to the four lateral toes. The increasingly reduced fleshy bellies form fine tendons which cross on the plantar side of the deep transverse metatarsal ligaments and then end by fusing with the tibial half of the dorsal expansions of their respective toes. This blending takes place over the proximal half of the first phalanx. The lumbricales are essentially the same in *Alouatta fusca* except that an additional attachment to the proximal phalanx of each of the last four toes is indicated (Sirena, 1871).

Nerve supply: The first lumbrical was innervated by the first common digital branch of the medial plantar nerve in both sides of the female, and in two of the males. Lumbricales to the third, fourth, and fifth toe were supplied by the deep branch of the lateral plantar nerve in these three specimens. All four lumbricales were innervated by the deep branch of the lateral plantar nerve in the remaining male.

Function: Flexion of the metacarpophalangeal joint.

DEEP SERIES, SUPERFICIAL LAYER

This layer is invariably represented by an adductor to the hallux and contrahentes to the second, fourth, and fifth toes.

M. adductor hallucis: This is a massive and roughly triangular muscle in the central compartment of the foot (fig. 48). Its base lies along the central axis and corresponds to its origin. The belly thickens considerably toward the insertion.

Caput obliquum arises from the third cuneiform and the proximal half of a sagittal aponeurotic septum attached along the middle of the third metatarsal. Fibers from the cuneiform are initially fibrous and oriented distomedially, those from the septum are fleshy and increasingly transverse in direction. This head is fused along its dorsomedial border with the fibular head of the flexor hallucis, the two muscles having a firm common and fleshy insertion on the fibular

side of the capsule of the first metatarsophalangeal joint. There is a sesamoid bone near this ending within the fibers of the combined bundles.

The caput transversum begins by fleshy fascicles from the distal half of the same sagittal septum and the deep transverse metatarsal ligament of the second interspace. They run transversely toward their insertion along the fibular side of the two hallucal phalanges. Sirena notes the strong development of the muscle, particularly the transverse head.

Nerve supply: A branch from the deep ramus of the lateral plantar nerve.

Function: Abduction of the hallux.

Mm. contrahentes digitorum pedis: Three such muscles are present (fig. 48). Those for toes IV and V are lateral to the axial origin of m. adductor hallucis; that of the fourth toe is covered proximally by the belly of contrahens V and that of the second toe entirely by the adductor hallucis. These three muscles arise from the sagittal septum of metatarsale III by aponeurotic fibers whose fleshy continuations form their respective fusiform and plantarly flattened bellies. The origin extends proximally to the fibrous sheath of the peroneus longus and in the lateral half of the tarsus to the lateral cuneiform bone. Insertion is on the medial base of the proximal phalanx in toes IV and V, and on the lateral side in toe II. Sirena (1871) describes contrahentes to toes II, IV, V and an adductor to the hallux with comparable origins and insertions to those described here.

Nerve supply: The deep branch of the lateral plantar nerve travels deep to the three muscles and sends branches which enter them on their deep surface.

Function: They adduct the lateral and medial toes toward the third digit.

DEEP SERIES, DEEP LAYER

M. flexor hallucis brevis: Caput tibiale (fig. 48) is a well-developed muscle arising by long tendinous fibers from the plantar surface of the second cuneiform and the sheath of the long peroneal tendon. They pass medially toward the base of the first metatarsal and give origin to the fleshy fibers of the muscular belly. This runs distally over the plantar and tibial side of metatarsale I covered by the tendon of the abductor hallucis, to which some of its fibers are attached. Insertion takes place together with that tendon on the tibial base of the first hallucal phalanx. Its fibers are closely connected to the underlying capsule of the first metatarsophalangeal joint.

Caput fibulare is entirely associated with the oblique head of the adductor hallucis, of which it appears to form a third part (fig. 48) differentiable only by its nerve supply. The origin is by tendinous

fibers from the plantar surface of cuneiforme I. These shortly become fleshy and pass distally along the peroneal side of metatarsale I. The belly is covered here by the caput tibiale and by the oblique adductor, with which it appears to form a single body. Insertion is by fleshy fibers together with the oblique head of the adductor hallucis on the lateral side of the first metatarsophalangeal capsule. The fibular head is fixed to the first metatarsal by fleshy fibers attached all along the shaft of this bone. Sirena (1871) states that the flexor hallucis brevis in *Alouatta fusca* is just like that of man.

Nerve supply: Both heads of the muscle are innervated by the medial plantar nerve.

Function: Flexion of the first metatarsophalangeal joint and adduction of the metatarsal.

Mm. interossei pedis: These are arranged into four dorsal and three plantar muscles (fig. 45). The former have a double origin from the adjacent metatarsals between which they lie; each of the latter arises only from the metatarsal of the toe upon which it acts. The caput tibiale of the first dorsal interosseous is small and its fleshy fibers come from the base of the first metatarsal on its fibular side. It soon joins the larger caput fibulare which has a more extensive origin from the entire tibial side of the base and shaft of metatarsale II. The muscular belly forms a tendon over the tibial side of the second metatarsophalangeal joint. It lies here covered by the fibers of the dorsal extensor expansion that reach the capsule of the joint. Insertion takes place by joining that expansion and partly on the tibioplantar base of the first phalanx of II. The origin of the second dorsal interosseous is from the proximal half of the dorsal border in the shaft of metatarsale II and the entire tibial half of the shaft and base of metatarsale III. The tendon formed by its belly at the tibial side of the third metatarsophalangeal joint is also largely joined to the overlying dorsal extensor expansion; the rest is inserted on the tibioplantar base of the proximal phalanx of III. For the third dorsal interosseous the origin is from most of the dorsal border of metatarsale III. Insertion is by a transversely compressed tendon on the fibuloplantar base of the first phalanx in toe III and by most of its fibers on the corresponding dorsal extensor expansion of III. The fourth arises from the proximal half of the dorsal border of metatarsale V and the entire fibular half of the shaft and base of metatarsale IV. Insertion takes place partially on the fibuloplantar base of the first phalanx of toe IV and into the dorsal expansion.

Origin of the first plantar interosseous is from the peroneal half of the shaft and base of metatarsale II. Its fleshy fibers run distally and form a transversely flattened tendon whose insertion is on the fibular half of the base in the first phalanx of toe II deep to the ending of m. contrahens II. At this point its tendon fuses with those fibers of the

dorsal expansion that reach the capsule of the corresponding metatarsophalangeal joint. The second plantar interosseous arises from the tibial half of the shaft and base of metatarsale IV. Its fibers end by a tendon in the same side of the base of the first phalanx of toe IV. The same relation exists here with the dorsal extensor expansion and contrahens IV. The third plantar interosseous originates from the tibial shaft and base of metatarsale V and is inserted by a tendon on the tibioplantar base of the first phalanx of toe V. There are equivalent relations to m. contrahens IV and the dorsal extensor expansion. The same muscles in *Alouatta fusca* (Sirena, 1871) present no significant difference.

Nerve supply: All of them are supplied by branches of the deep ramus of the lateral plantar nerve.

Function: Dorsal interossei abduct the medial and lateral toes from the third digit. In view of their respective relations with the dorsal extensor expansions, the dorsals are also extensors of the metatarsophalangeal joints, whereas the plantars are flexors. The latter adduct toes II, IV and V toward the third digit.

M. flexor digiti quinti (=flexor digiti minimi brevis of N.A.): It lies on the fibular and plantar side of the fifth metatarsal and is not as well developed as m. abductor hallucis, but it is still a strong muscle (fig. 48). Origin is by a mixture of fleshy and tendinous fibers from the plantar surface of the base of metatarsale V, cuboideometatarsal joint, and the cuboid bone. Its fibers appear to be a continuation of those of the calcaneocuboidal ligament. As it passes over the lateral aspect of the metatarsal it picks up additional fibers from the shaft of this bone. The muscle continues its course to reach the peroneal base of the first phalanx in the fifth toe. It ends here after fusing with the capsule of this metatarsophalangeal joint. Many of its fascicles are inserted on the tendon of m. abductor digiti V which passes through the center of the flexor belly. The muscle in *Alouatta fusca* (Sirena, 1871) presents no difference.

Nerve supply: The deep branch of the lateral plantar nerve sends a branch to the muscle before passing medially under the layer of the contrahentes muscles.

Function: It flexes the fifth toe and, because of its insertion on the peroneal base of its first phalanx, simultaneously contributes to its abduction.

M. opponens hallucis: This is well differentiated and well developed, lying between both parts of m. flexor hallucis brevis and the first metatarsal (fig. 48). Origin is by long tendinous fibers in common with those of the short flexor from the second cuneiform and the peroneal sheath. The fleshy fibers spread fanwise over the metatarsal to insertion along the tibial margin of its shaft. Sirena (1871) does not mention this muscle at all.

Nerve supply: Deep ramus of the lateral plantar nerve.

Function: It brings the hallux into opposition with the other toes.

Comparative anatomy of the pedal group.—The available literature dealing with the pedal muscles of the platyrrhine genera we are considering is scarce. Hill (1962) is the exception, as he covers them all, particularly in the case of *Brachyteles*, in more detail. From the information on hand, it appears as if most of these muscles in the foot of all the prehensile-tailed ceboids conform to a common pattern. This applies especially to the hallux and fifth-digit musculature.

Only contrahens I and II are reported for *Lagothrix*, I, II, and IV for *Brachyteles*, where they are said to correspond to the "c" pattern of Jouffroy and Lessertisseur (see Hill, 1962). Ruge (1878b) studied this layer in *Cebus apella* and *Ateles paniscus* and found a full set of contrahentes in both genera; the origin of m. adductor hallucis, caput transversum differed, however, in each genus. He described it in the spider monkey as arising from (1) the distal half of the lateral margin m. contrahens II, (2) the capsules of the second and third tarsometatarsal joints, and (3) the medial surface of caput metatarsale II. I suspect a printing error when he says, "Tarsometatarsalgelenkes" where perhaps he meant metatarsophalangeal instead. The origin of m. adductor hallucis in *Cebus* (Ruge, 1878b) is by two tendinous bands from the capsules of the second and third metatarsophalangeal joints. The oblique head in this genus covers the origin of m. contrahens II, but in *Ateles* this overlap is reduced to the proximal third of contrahens II. The distribution of tendons from both heads of the flexor digitorum brevis in all these animals (Glaesmer, 1910; Hill, 1962; Sawalischin, 1911) is highly variable. None of the patterns has a consistent distribution for a given genus. The deep head is absent in the woolly spider monkey, and its interossei are said to be eight: namely, four dorsals and four ventrals (Hill, 1962).

Conclusions

The combination of muscular characteristics that I have just described in the red howling monkey is one among the series of adaptations which this genus has developed in adjusting to a certain mode of life in a given environment. That vocal communication is, and has been, an important aspect of the habits of this animal is a fact supported by behavioral field studies (Altmann, 1959; Carpenter, 1934, 1960) and by the anatomical evidence of the greatly enlarged hyolaryngeal organs of the neck.

The larynx, hyoid, and related structures attain an enormous size in both sexes of adult howlers. The sounds produced by this apparatus

are amplified in a system of air sacs, but the role of these chambers as resonators is not yet well understood. The enlarged hyoid bone, which is filled by a tube-like membranous expansion of the laryngeal lining, strongly suggests that this bulla is an important resonator.

The evolution of these massive organs in the neck of *Alouatta* has very strongly influenced the morphology of the structures around the hyoid and the larynx, and in addition, it seems quite reasonable to conclude that it has also effected changes in other parts of the body. Thus, the acquisition of these anatomical specializations for voice production appear to have led to mechanical problems that had to be solved by the gradual development of adaptations in the locomotor system. I suspect that the peculiar combination of skeletal characteristics, such as one finds in *Alouatta*, is an expression of these adaptations: (a) A relatively high intermembral index (Humerus+Radius/Femur+Tibia) of 98, a value closer to those of *Ateles* (105), *Brachyteles* (105), and *Lagothrix* (98) than to that of *Cebus* (80) (Erikson, 1963); (b) the forelimb index value (Humerus+Radius/Trunk Vertebral Column) in *Alouatta* of 91 is very close to that of *Cebus* (90), but, separated by 17 units from the value of 109 for *Lagothrix*, and even further removed from those of *Ateles* (150) and *Brachyteles* (140) (Erikson, 1963); (c) the lumbar segment of the vertebral column in *Alouatta* seems to be the longest among the brachiator monkeys of the New World (Erikson, 1963); (d) a comparison of the scapulas of *Alouatta*, *Ateles*, *Brachyteles*, and *Lagothrix* (see Erikson, 1963, plate 3A) reveals that it is the bone of the howler which most closely resembles that of a quadruped (it has a moderately large acromion and its spine has only a slight obliquity in relation to the vertebral border; in addition, the glenoid of the scapula in the howler does not seem to face as much craniad as in the other brachiators); (e) the supraspinous fossa of *Alovatta* appears to be very large (Erikson, 1963; Hill, 1962; Schultz, 1930). Moreover, several muscles of the trunk and limbs seem also to have been affected in connection with the modifications that occurred in the locomotor system.

The howlers are described (Carpenter, 1934, 1960) as arboreal quadrupeds moving in the highest branches of the trees by using their limbs and prehensile tails in a deliberate and carefully aimed manner. Not infrequently they make short jumps between close branches. The animals propel themselves with the hind limbs and the extended arms secure a hold on the landing place. This quadrupedal locomotion is favored by the fact that the displacement backward of the foramen magnum brings the axis of the orbits almost in line with the direction in which the animal will be advancing. Other prehensile-tailed cebids are probably forced to extend their

necks in order to face forward when standing or walking on their four extremities. That the change in position of the foramen magnum is due to the modifications of the hyolaryngeal structures has been clearly shown by Leche (1912) and Biegert (1963). Such an arrangement is, nevertheless, an enormous hindrance to brachiation. The fact that *Alouatta* rarely hangs by its arms indicates how difficult it should be for this animal to move in a manner even faintly reminiscent of that practiced by the spider monkey. In spite of this fact, the howler shares many details of its musculature with *Ateles*, *Brachyteles*, and *Lagothrix*. The resemblance is striking in those characters which, in at least the first two, are regarded as specializations to their brachiating habits. The machinery to brachiate, so to speak, is there, even if the howlers do not use it but practice a quadrupedal locomotion. This habit is reflected in the presence of several traits indicative of pronograde stance and movements.

I shall now discuss the regional adaptations of the musculature in *Alouatta*. For further details the reader is referred to the sections dealing with particular muscles and muscular groups.

Adaptations in the musculature of the head.—The outstanding characteristic of the muscles in the trigeminal group of the howler is the pronounced size (figs. 1 and 4). The enlargement, as compared with other cebids, must be related to the general process of expansion that has taken place in the hyolaryngeal organs and which also has affected the mandible. The mandibular insertion of m. digastricus is peculiar in that it does not reach beyond the level of M_2 (fig. 2). It is interesting to note that in this respect there is a resemblance with the condition of the muscle as described by Duckworth (1915) and Murie and Mivart (1872) in lemuroids. I am not yet in a position to judge whether this character in *Alouatta* is a primitive one retained from a prosimian ancestor, or a specialization of the howler whereby the digastricus has apparently withdrawn its mandibular attachment dorsally in order to leave room, so to speak, for the expanding bulla hyoidea.

The arrangement of the facial muscles seems to have advanced phylogenetically to a stage comparable to that of the Atelinae, but the extensive development of the platysma colli et faciei which forms a continuous muscular layer with the orbitozygomatic plate is perhaps a specialization of *Alouatta* conditioned by the exaggerated growth of the mandible (fig. 6). The variable presence of a triangularis, an apparent constant feature in *Ateles*, *Brachyteles*, *Lagothrix*, and *Cebus* (see Ruge, 1887; Schreiber, 1928; Hill, 1962) suggests that this is a structure which has not yet attained a definite pattern, probably, because of the growth influences affecting the area where the muscle is located.

The stylopharyngeus and other muscles of the pharynx have also undergone a considerable increase in size (fig. 8). The variability manifested in the glossopharyngeal part of the superior constrictor of the pharynx is comparable to that of the triangularis. The importance of the middle constrictor, pars membranacea, with relation to the emptying of the air sacs, and of the inferior constrictor in a similar role, and in the control of the vocal cords, has been discussed when dealing with these muscles.

Of the muscles operating on the hyoid bone (fig. 3), some belong to the facial group, as m. stylohyoideus; others to the lingual, as m. genioglossus, m. hyoglossus, and m. styloglossus; the rest to the ventral group of hypaxial muscles, as m. sternohyoideus and m. thyrohyoideus. They all present a remarkable increase in size and in addition the styloglossus was absent in two out of five specimens I examined (this report; Schön, 1964a). That the styloglossus does not substitute functionally for the glossopharyngeal part of the superior constrictor is evident from the fact that when the first is lacking the second is not found either. The importance of the stylohyoideus was dealt with previously (Schön, 1964a).

The muscular differences summarized so far between the howler and other prehensile-tailed cebids are either directly related to the production and modification of the voice of the howler or depend on the overall growth process affecting its hyolaryngeal parts and extending into the surrounding area.

Adaptations in the musculature of the trunk.—Some of the modifications encountered in these muscles of the howler, particularly in the epaxial group, I believe to be related to the need for more powerful extensors of the neck. The scarcity of comparative information calls for caution in accepting the following conclusions. The subdivisions of the epaxial muscles in *Alouatta* are only moderately differentiated. The arrangement of its erector spinae (fig. 13) can be compared to that observed by Howell and Straus (1933) in the rhesus monkey. It suggests a rather rigid body in the sense that its vertebral column and associated muscles do not allow great freedom for lateral rotation over this axis. I am unfortunately in no position at the present time to say whether this pattern is more typical of a quadruped than of a brachiator monkey of the New World. The dorsal muscles in the neck have details which are perhaps related to their role as extensors. A combined longissimus capitis et cervicis (fig. 14) and a spinalis et semispinalis capitis (fig. 15) might be adaptations to this function in the nuchal region where the need for strong extensors is evident. One cannot discount the very likely explanation that the combined bellies of these otherwise separate muscles is merely a generalized primate character. The peculiar arrangement of the

cervical interspinals and the corresponding changes in the spinous processes of the region are more clearly dependent on the needs for keeping the neck extended.

It should now be said that the epaxial muscles, as well as the ventral ones, are highly organized in the tail of *Alouatta;* but probably not to a greater degree than in other prehensile-tailed monkeys.

It is interesting to note that the scalenus brevis posterior of the lateral group of hypaxial muscles has a variable development in different specimens of howlers. Its location (fig. 17) allows it to act as an additional extensor of the cervical spine and it appears as a robust and well-developed column in some cases, but as an inconspicuous longitudinal bundle in others. This variability indicates that the pattern of the muscle is as yet not definitely set.

Of the muscles in the ventral group, the sternohyoideus, sternothyroideus, thyrohyoideus, costothyroideus, and geniohyoideus are considerably enlarged (fig. 3) in relation to *Cebus* and the Atelinae. They are of importance in keeping the hyolaryngeal structures in place and perhaps also in modifying the voice. Contraction of the sternohyoideus might help to close the hyolaryngeal canal by pressing the bulla against the epiglottis and also to empty the saccules by its action against the thyroid lamina (see fig. 11 in Schön, 1964a). The sternothyroideus and costothyroideus lower the thyroid cartilage. The second muscle may, in addition, contribute to the inrush of air into the sacs and canal by pulling apart the upper margins of the plates. The thyrohyoideus is possibly an antagonist of the costothyroideus in that its contraction shortens the distance between the cornu branchiale I and the thyroid cartilage, therefore emptying the air sacs. The functional significance of the geniohyoideus was discussed elsewhere (Schön, 1964a). The subvertebral and perineal groups do not offer significant differences from those of *Ateles*, *Cebus*, and *Brachyteles* (see von Eggeling, 1896; Forster, 1926; Elftman, 1932; Hill, 1962).

Adaptations in the musculature of the upper extremity. — The shoulder region of *Alouatta* is of great importance for the elucidation of the locomotor changes imposed on this animal by the increase in size of the structures related to the production of voice. An interesting combination of muscular characteristics typical of the New World brachiators (see Campbell, 1937) with other details indicative of quadrupedal locomotion (see Ashton and Oxnard, 1963) are to be found in the pectoral girdle of the howler. Also, some of the shoulder muscles which participate in the extension of the neck have undergone modifications.

The trapezius is a muscle of the vago-accessory group of the head and together with the caudal part of the serratus anterior, it is an important elevator of the shoulder (see Oxnard, 1963). The muscle

has extended its insertion beyond the acromion on to the clavicle in *Ateles* (Ashton and Oxnard, 1963, Campbell, 1937; Hill 1962), *Brachyteles* (Hill, 1962), *Lagothrix* (Ashton and Oxnard, 1963; Campbell, 1937; Hill, 1962; Robertson, 1944), and *Alouatta*, but only in the howler is its cranial origin extensive (table 1). It extends from the occipital protuberance to the middle of the nuchal crest (fig. 5). This character I regard as an adaptation of the trapezius to act as an extensor of the neck. The greater thickness of the cranial portion of the muscle is another detail in common with the Atelinae.

TABLE 1.—*Data for* Cebus (*climber or quadruped*), Lagothrix, Brachyteles, *and* Ateles (*brachiators or semibrachiators*) *and* Alouatta* (Pluses=degree of development: +++=larger, ++=intermediate, +=lesser, ?=unknown.)

Characteristics	*Cebus*	*Alouatta*	*Lagothrix*	*Brachyteles*	*Ateles*
Clavicular insertion of m. trapezius	Absent	Present	Present	Present	Present
Cranial part of m. trapezius thicker than the caudal part	No	Yes	Yes	Yes	Yes
Extension of nuchal origin of m. trapezius	+	+++	+	+	+
M. atlantoscapularis anterior is inserted mainly in the clavicle	No	Yes	Yes	Yes	Yes
Development of caudal part of m. serratus anterior, pars caudalis	+?	++	+++?	+++?	+++?
Large, undivided craniocervical part of m. rhomboideus	No	Yes	No	No	No
Extensive occipital origin of m. rhomboideus	No	Yes	No	No	No
Ventral fibers of m. latissimus dorsi have perpendicular direction	No	Yes	?	?	?
M. latissimus dorsi arising mainly from spinal column	Yes	No	No?	No?	No?
Origin of m. teres major occupies a large area near caudal angle	Yes	Yes	No?	No?	No?
M. pectoralis major has a clavicular head	No	Yes	Yes	Small	Absent or reduced

*Summarized from Ashton and Oxnard, 1963; Campbell, 1937; Hill, 1960, 1962; Robertson, 1944; Schück, 1913a; Sirena, 1871; this work.

TABLE 2.—*Comparison of the cranial limit of the origin of m. serratus anterior, pars caudalis between* Alouatta *and locomotor groups (data for semibrachiators and quadrupeds taken from Ashton and Oxnard, 1963; for* Alouatta, *this work.)*

	No. of specimens	Rib number						
		1 %	2 %	3 %	4 %	5 %	6 %	7 %
Quadrupeds	100			5. 0	24. 0	69. 0		2. 0
Semibrachiators	10		50. 0	50. 0				
Alouatta	4			100. 0				

Significance of difference in mean cranial limit of origin of m. serratus anterior, pars caudalis; semibrachiators and quadrupeds: $p<0.001$.

It is interesting to note that the broad occipital origin of the muscle occurs also in other primates where the extension of the neck acquired particular importance in view of the presence of a large masticatory apparatus, *Gorilla*, *Papio*, *Comopithecus*, and *Mandrillus* (see Ashton and Oxnard, 1963). The acromioclavicular ending of m. atlantoscapularis anterior superficial to the trapezius is another character of *Alouatta* in common with *Ateles*, *Brachyteles*, and *Lagothrix*, but absent in the quadrupedal *Cebus* (see Ashton and Oxnard, 1963; Campbell, 1937; Hill, 1960, 1962; Robertson, 1944) (table 1).

The caudal part of the anterior serratus shows a curious mixture of characters (fig. 17). Being not too thick, it resembles that of the capuchin monkey (table 1). The cranial limit of its origin on rib 3 places the howler right at the point of overlap between the quadrupeds and the semibrachiators of Ashton and Oxnard (1963), the latter group including the spider and woolly monkey (table 2); however, in the number of ribs spanned, *Alouatta*, with six, clearly falls within the range of the quadrupeds (4–7) rather than among the semibrachiators (7–11) (table 3).

In the deltoideus, which is an elevator of the arm, the pars spinalis was separated from the rest of the muscle bilaterally in one male. In this respect the howler slightly resembles the quadrupedal monkeys (see Ashton and Oxnard, 1963).

The rhomboideus, a stabilizer of the shoulder, and m. atlantoscapularis posterior, an elevator of the shoulder, are enlarged in relation to their possible increased significance in extending the neck (fig. 25). There is no separation of the rhomboideus into two parts as in the case of the semibrachiators and quadrupeds (see Ashton and Oxnard, 1963), and the occipital origin of the muscle is wider and thicker than in any other cebid under consideration (table 1). These characters conform with what would be expected if the muscle indeed acts as

TABLE 3.—*Comparison of m. serratus anterior between* Alouatta *and locomotor groups (data for semibrachiators and quadrupeds taken from Ashton and Oxnard, 1963; for* Alouatta, *this work).*

	No. of specimens	Number of Ribs Spanned							
		4 %	5 %	6 %	7 %	8 %	9 %	10 %	11 %
Quadrupeds	100	14. 0	29. 0	56. 0	1. 0				
Semibrachiators	10				10. 0	40. 0	20. 0	10. 0	20. 0
Alouatta	4			100. 0					

Significance of difference in mean numbers of ribs spanned by m. serratus anterior, pars caudalis; semibrachiators and quadrupeds: $p < 0.001$.

a rather constant extensor of the neck in *Alouatta*. A caudal limit for its spinal insertion on T4 places the howler in the modal value for the quadrupeds of Ashton and Oxnard (1963) (table 4). This figure, I should add, corresponds to one end of the range of their semibrachiators (T4–T8). The atlantoscapularis posterior has been often described as the pars cranialis of the serratus anterior. I agree that in the howling monkey the muscle might be regarded as merely the highest digitation of the serratus; but because of its scapular attachment and the presumed importance which the muscle might have in *Alouatat* as an extensor of the neck, I decided to treat it separately. The traction exerted by the atlantoscapularis posterior on its supraspinous anchorage might be the factor responsible for the peculiarly extensive fossa in *Alouatta*.

The partly quadrupedal and brachiating characters of the howler are very evident in those muscles which act as propulsors of the upper extremity. The cranial limit for the origin of m. latissimus dorsi puts *Alouatta* in the region of overlap between quadrupeds (T4–T8) and the semibrachiators (T6–T10) (table 5). The expansion of the muscular attachment into the rib cage averages four slips in seven specimens of *Alouatta* (4 mine; 3 of Sirena, 1871). The average in *Cebus* is four ribs (see Schück, 1913a). The number in *Lagothrix* is not clear but *Brachyteles* appears to have six (Hill, 1962), and *Ateles* six (Schück, 1913a). The development of this muscle in the howler did not impress me as robust, but the almost perpendicular direction of its ventral fibers reminds one of the condition in *Ateles* (table 1). The origin of m. teres major occupies a large area near the angle, a character attributed by Ashton and Oxnard (1963) to the muscle in quadrupeds (table 1). The strong development of the triceps brachii bears witness to the importance of this muscle in the extension of the arm.

TABLE 4.—*Comparison of the caudal limit of the origin of m. rhomboideus between* Alouatta *and locomotor groups (data for semibrachiators and quadrupeds taken from Ashton and Oxnard, 1963; for* Alouatta, *Sirena, 1871, and this work).*

	No. of specimens	Thoracic Vertebra Number					
		3 %	4 %	5 %	6 %	7 %	8 %
Quadrupeds	48	8. 3	33. 3	25. 0	25. 0	8. 3	
Semibrachiators	20		5. 0	25. 0	20. 0	40. 0	10. 0
Alouatta	7		100. 0				

Significance of difference in mean caudal limit of origin of m. rhomboideus; semibrachiators and quadrupeds: $p < 0.001$.

The pectoralis major of *Alouatta* possesses a clavicular head (fig. 31) (table 1). This part of the muscle is said to be small in *Brachyteles* (Hill, 1962), but absent (Campbell, 1937) or reduced (Hill, 1962) in *Ateles*. It is present in *Lagothrix* (Ashton and Oxnard, 1963; Campbell, 1937; Hill, 1962; Robertson, 1944). The howler resembles the semibrachiators of Ashton and Oxnard (1963) in the strong development of the sternoclavicular part of the muscle, but contrasts with their quadrupeds whose sternocostal portion is the larger and extends more caudally down to about the eighth costal cartilage. The pectoralis minor of *Alouatta* arises from costal cartilages 3–5, resembling all prehensile-tailed cebids except *Cebus* whose muscle comes from the sternum (see Ashton and Oxnard, 1963; Campbell, 1937; Hill, 1960, 1962; Robertson, 1944).

The rest of the forelimb muscles appear to conform to a similar pattern in *Alouatta*, *Ateles*, *Brachyteles*, and *Cebus*. The pertinent literature about the last four animals is cited in the sections dealing with the muscles of this extremity. The subdivision of the deep digital extensor seems to show great variability among these genera, but this situation might be the result of incomplete observations on the part of the researchers concerned, rather than true differences. The separation of that muscle into a belly supplying tendons for the index and pollex, and another head for the middle finger might be one of the anatomical bases for the kind of manual grasp observed in the howler. The extent of the radial insertion of the pronator teres in *Cebus*, an arboreal quadruped, is shorter than in *Alouatta*, *Ateles*, *Brachyteles*, and *Lagothrix*.

ADAPTATIONS IN THE MUSCULATURE OF THE LOWER LIMB.—The muscular pattern of this extremity in *Alouatta* more closely resembles that of the Atelines than that of *Cebus*, even if the similarities among

TABLE 5.—*Comparison of the cranial limit of the origin of m. latissimus dorsi between* Alouatta *and locomotor groups (data for semibrachiators and quadrupeds taken from Ashton and Oxnard, 1963; for* Alouatta, *Sirena, 1871, and this work).*

	No. of specimens	Thoracic Verbebra Number						
		4 %	5 %	6 %	7 %	8 %	9 %	10 %
Quadrupeds	59	42. 4	18. 6	8. 5	20. 3	10. 2		
Semibrachiators	13			7. 7	23. 1	46. 1	15. 4	7. 7
Alouatta	7				14. 3	28. 6	57. 1	

Significance of difference in mean cranial limit of origin of m. latissimus dorsi; semibrachiators and quadrupeds: $p < 0.001$.

all five are very evident. The most remarkable character of the howler, I think, relates to the function of its gluteus medius in keeping the trunk semi-erect when the animal sits on its haunches (figs. 41 and 42). This point is discussed extensively in the section covering that muscle. There is an interesting detail about m. gluteus maximus which should be mentioned. Klaatsch (1900) asserts that it is stronger in the howler than either *Ateles* or *Lagothrix*. Bodini (1965) has shown in her studies still in progress that the ectogluteus of the capuchin is larger than in any other monkey with prehensile tail. These observations put *Alouatta* in a sort of intermediate position between *Cebus* and the Atelinae, and might, therefore, indicate an adaptation to arboreal quadrupedalism, a kind of locomotion where the lower members are the main propulsors of the body.

With respect to the hamstring muscles one gets the impression from the current research by Bodini (1965, personal communication) that these muscles are better developed in the howler than in the spider monkey, but less so than in *Cebus*. This one would expect from *Alouatta* if it indeed practices quadrupedalism as its main form of locomotion.

The special interest that attaches to the howler monkey is based on the fact that although it is known to be essentially an arboreal quadruped (Carpenter, 1934, 1960), its musculature is mainly that of a New World brachiator with, however, some quadrupedal characters. The animal has, in addition, several muscular specializations of its own in relation to the production and modification of voice. The following lines of reasoning perhaps may help to explain this peculiar combination of morphological characters and locomotor habits.

During the middle or early Cenozoic some of the New World primates presumably had invaded the higher branches of the trees,

where they moved by using the slender vines as supports. This group of animals included the ancestors of present day *Ateles*, *Brachyteles*, *Lagothrix*, and *Alouatta*. The locomotor system developed structural adaptations in accord with arboreal habits. A common genetic background and the same selective forces were responsible for the acquisition of the same muscular pattern, very significantly in the shoulder region, as a response to the needs for brachiation. Presumably when the howler line branched off, the increase in size of the hyolaryngeal organs introduced new mechanical problems for the locomotor system. The changes in the neck severely restricted the ability of these early howlers to progress through swinging by their arms. They had to revert to quadrupedal habits and either reversed some of their muscular arrangements or retained those which had not yet become fully adapted for brachiation. The latter seems the simpler explanation. The paleontological evidence (Stirton, 1951) is suggestive of an early separation of the howlers from the Atelines, but, unfortunately, it is not conclusive.

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Alphabetical Listing of Muscles

M. abductor caudae lateralis, 39
M. abductor caudae medialis, 39
M. abductor digiti quinti manus (=abductor digiti minimi of N.A.), 116
M. abductor digiti quinti pedis (=abductor digiti minimi of N.A.), 160
M. abductor hallucis, 159
M. abductor ossis metatarsi quinti, 162
M. abductor pollicis brevis, 113
M. abductor pollicis longus, 96
M. adductor brevis, 147
M. adductor hallucis, 162
M. adductor longus, 146
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M. adductor pollicis, 117
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